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THE INHERITANCE OF RUST RESISTANCE. II. THE INHERITANCE OF STEM RUST RESISTANCE IN SIX ADDITIONAL VARIETIES OF COMMON WHEAT[1]

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ABSTRACT

The inheritance of resistance to races 15B and 56 of stem rust was studied in the varieties Africa No. 43, Kenya C9906, Kenya 338.AC.2.E.2, Egypt Na101, Veadeiro and Red Egyptian type (P.I. 170910). Each variety was analysed genetically on the basis of data obtained from a backcross to the rust susceptible variety Marquis. The interrelationships of the genes in the varieties were determined from diallel crosses. With the exception of Veadeiro, the varieties all carried various combinations of genes reported in the first paper of this series. Veadeiro has a mature plant resistance to race 15B which is probably conditioned by two additive genes not previously noted.

INTRODUCTION

In the first paper of this series, Knott and Anderson (2) reported on the inheritance of resistance to races 15B and 56 of *Puccinia graminis tritici* Eriks. and Henn. in ten varieties of *Triticum vulgare* Vill.—Kenya 58, Kenya 117A, Red Egyptian, Egypt Na95, McMurachy, Gabo, Lee, Timstein, Thatcher and Marquis. The work with these two races now has been extended to include the varieties Africa No. 43, Kenya C9906, Kenya 338.AC.2.E.2 (Kenya Farmer), Egypt Na101 (Kenya Governor), Veadeiro and Red Egyptian type (P.I. 170910). This second group of varieties was selected to include as many countries of origin as possible in the hope that new genes for resistance to races 15B and 56 might be discovered. As in the first set of varieties, Marquis was included as a rust susceptible parent and Thatcher as a parent for plant breeding purposes. Red Egyptian was added in an attempt to relate the genes in the new varieties to some of those carried by the first set of varieties.

REVIEW OF LITERATURE

Very little literature is available on the varieties studied. As far as is known, nothing has been published on the inheritance of stem rust resistance in Africa No. 43, Kenya C9906, Egypt Na101, Veadeiro and Red Egyptian type (P.I. 170910). Smith (4) reported that in Kenya 338. AC.2.E.2 the inheritance of resistance to race 15B is relatively simple,

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but no analysis of the results was made. Kenya 338.AC.2.E.2. has recently been named Kenya Farmer by Thorpe (6). The literature on Thatcher and Red Egyptian has been summarized by Knott and Anderson (2). Thatcher has been reported to have either two or three recessive genes for rust resistance. Red Egyptian has two genes, *Sr6 and Sr8*, which condition resistance to both races 15B and 56 and one, *Sr9*, which conditions resistance to race 56. Marquis is susceptible to both races. Of the nine varieties, four, Africa No. 43, Egypt Na101, Kenya C9906 and especially Kenya 338.AC.2.E.2, are being used as sources of rust resistance in wheat breeding programs in various countries.

MATERIALS AND METHODS

A brief description of the varieties studied, with particular reference to their rust resistance, is given below:

Africa No. 43 (*P.I. 159106*) came from South Africa. It has good resistance to races 15B and 56, although its resistance breaks down at high temperature. It is also resistant to leaf rust.

Kenya C9906 (*P.I. 118896*) has good resistance to races 15B and 56, but the resistance tends to break down at high temperature.

Kenya 338.A.C.2.E.2 (*P.I. 187165*) has been used extensively as a source of rust resistance. Until now, it has been resistant to all races of stem rust to which it has been subjected in North America, and its resistance does not break down at high temperatures. It is also resistant to leaf rust.

Egypt Na101 (*P.I. 139599*) is apparently an Egyptian designation for the variety Kenya Governor. Although the variety has good resistance to race 15B, it is moderately susceptible to race 56. Egypt Na101 is one of the few varieties which have resistance to race 189 of stem rust.

Veadeiro (*P.I. 192475*) is a Portuguese variety which has fair resistance to races 15B and 56 and is also resistant to leaf rust. Its resistance to race 15B is of the mature plant type.

Red Egyptian (*C.I. 12345*) apparently originated in Ethiopia. It has good resistance to races 15B and 56 except at high temperatures.

Red Egyptian type (*P.I. 170910*) is a variety of South African origin. Despite its name, it is quite different from Red Egyptian in appearance, but it is similar in rust resistance. To avoid confusion with Red Egyptian, the variety will be designated by its P.I. number in the remainder of this paper.

Thatcher (*C.I. 1003*), as reported by Hayes *et al.* (1), was developed at the University of Minnesota from the cross (Marquis × Iumillo) × (Kanred × Marquis). It has moderate resistance to race 56, but is susceptible to race 15B.

Marquis (*C.I. 3641*) was developed at Ottawa from the cross Hard Red Calcutta × Red Fife. It is susceptible to both race 15B and race 56.

Seed of the first six varieties was obtained from the United States Department of Agriculture, Plant Industry Station, Beltsville, Maryland. Marquis and Red Egyptian came from the University of Minnesota, and Thatcher from the University of Saskatchewan.

The methods used in these studies were similar to those described by Knott and Anderson (2). Diallel crosses were made between the nine varieties, except for the crosses between Red Egyptian, Thatcher and Marquis, which had been studied previously. The first six varieties, with the exception of Kenya 338.AC.2.E.2, were backcrossed to Marquis for genetic studies. All six varieties were also backcrossed to Thatcher, primarily as possible breeding material. The F_1 plants from the cross Kenya 338 × Marquis were sterile dwarfs and no backcross was possible.

A total of 33 crosses and 11 backcrosses were made. The crosses of Kenya 338.AC.2.E.2 with Africa No. 43, Marquis, Egypt Na101, Red Egyptian and P.I. 170910 produced only dwarf plants which were largely sterile, although a few seeds were obtained from the Africa No. 43 cross.

Rust tests were conducted on the various crosses and backcrosses as follows:

1. The F_1 plants from the diallel crosses were tested for field reaction to race 56 in 1953 and to race 15B in 1954.

2. The F_2 populations from the diallel crosses and the F_2 families from the backcrosses to Marquis were tested for field reaction to race 15B and seedling reaction to races 15B and 56.

3. The F_2 families from the backcrosses to Thatcher were tested for field reaction to race 15B.

The parents were included in all tests.

The methods of conducting rust tests were reported in the paper by Knott and Anderson (2) and will be described only briefly here. Field tests were carried out in an irrigated nursery. Rows planted to a mixture of susceptible varieties were used as rust spreaders. Plants in the "spreader" rows were inoculated with a suspension of spores of a single rust race by means of hypodermic needles. In addition, when moisture conditions were favourable, the plants were dusted with a mixture of spores and talc. For seedling tests, plants were grown in beds and inoculated by dusting the moistened leaves with the mixture of spores and talc. A canvas cover was fitted over the beds and kept wet to maintain a high humidity for 24 hours. In the tests on backcross families the seedlings were first

TABLE 1.—SUMMARY OF THE RESULTS OF RUST TESTS ON PARENTS AND F_2 POPULATIONS FROM THE DIALLEL CROSSES

	Variety and rust reaction	Race 56—seedling tests								
		A. 43 VR	K.C9906 VR	K.338 R	Na101 MS	Vead. R	170910 VR	R.E. VR	That. MR	Mar. S
Race 15B—seedling and field tests	Africa No. 43 VR		VR	Seg.	Seg.	Seg.	VR	VR	Seg.	3:1
	Kenya C9906 VR	VR		Seg.	Seg.	Seg.	VR	VR	Seg.	3:1
	Kenya 338 VR	Seg.	R-VR		D	R	D	D	Seg.	D
	Egypt Na101 R	Seg.	R-VR	D		Seg.	Seg.	Seg.	Seg.	S
	Veadeiro[1] R	Seg.	Seg.	Seg.	Seg.		R-VR	R-VR	Seg.	15:1
	P.I. 170910 VR	VR	VR	D	Seg.	Seg.		VR	Seg.	63:1
	Red Egyptian VR	VR	VR	D	Seg.	Seg.	VR		Seg.	63:1
	Thatcher S	Seg.	Seg.	Seg.	Seg.	Seg.	Seg.	Seg.		Seg.
	Marquis S	1:3	13:3	D	Seg.	Seg.	Seg.	13:3	S	

VR = very resistant, R = resistant, MS = moderately susceptible, S = susceptible, Seg. = segregating, D = dwarf F_1.

[1] Veadeiro is resistant in field tests but moderately susceptible in seedling tests.

TABLE 2.—RESULTS OF SEEDLING RUST TESTS ON F_2 FAMILIES FROM THE BACKCROSS OF AFRICA NO. 43 TO MARQUIS

		Race 15B		Totals (race 56)	Expected (1:1)	P
		Number of families				
		Seg.1VR:3S	S			
Race 56	Seg. 3VR:1S	42		42[1]	44.5	.50–.70
	S		47	47	44.5	
	Totals (race 15B)	42[2]	47	89	89	
	Expected (1:1)	44.5	44.5	89		
	P	.50–.70				

The ratios within segregating families were as follows:

Race 56
[1] 621VR:227S plants — P for a 3:1 ratio = .20–.30

Race 15B
[2] 225VR:669S plants — P for a 1:3 ratio = .90–.95

TABLE 3.—RESULTS OF RUST TESTS ON F_2 POPULATIONS FROM THE CROSSES AFRICA NO. 43 × MARQUIS AND AFRICA NO. 43 × RED EGYPTIAN

Cross and type of test		Number of plants		Ratio	P
		VR	S		
African No. 43 × Marquis F_2					
Seedling tests —race 56	Observed	106	31		
	Expected	102.75	34.75	3:1	.50–.70
Seedling tests —race 15B	Observed	37	85		
	Expected	30.5	91.5	1:3	.10–.20
Africa No. 43 × Red Egyptian F_2					
Seedling tests —race 56	Observed	137			
Seedling tests —race 15B	Observed	136			
Field tests —race 15B	Observed	185			

inoculated with race 15B and seven to nine days later with race 56. Previous tests showed that the first infection could be read and removed without interference from the second. In the tests on seedlings from the diallel crosses, separate samples from each F_2 population were tested with the two races. During the tests, greenhouse temperatures were kept sufficiently low to prevent a high temperature breakdown of the rust resistance.

Plants from field tests were pulled and the percentage rust was read for each plant, using the scale outlined by Peterson *et al.* (3). Rusted seedlings were read according to pustule type, using the system set up by Stakman *et al.* (5).

RESULTS

The actual data obtained from the various crosses will be given in the discussion of each variety. Since some of the data are repetitious and add nothing to the genetic analysis, they are omitted. A complete summary of the results of tests on the parents and F_2 populations from the diallel crosses is given in Table 1. Ratios are given for the Marquis crosses if the segregation was clearcut.

Africa No. 43

Africa No. 43 exhibits a hypersensitive type of seedling reaction to races 15B and 56 and has good resistance to race 15B in the field. The inheritance of its resistance to the two races proved to be simple.

The data from the backcrosses of Africa No. 43 to Marquis are given in Table 2 and the F_2 data from pertinent crosses are given in Table 3. Approximately half the backcross families segregated for a hypersensitive (fleck) reaction to both race 15B and race 56. Apparently, the same gene controls resistance to the two races. The gene is identical in action to the gene *Sr6*, previously identified in McMurachy, Kenya 58 and Red Egyptian. The ratios obtained within segregating backcross families and in the F_2 population from the cross Africa No. 43 × Marquis (Table 3) show that with race 15B the gene is recessive while with race 56 it is dominant. Thus with race 15B good fits were obtained to a ratio of 1 very resistant (fleck to type 1^-): 3 susceptible (type 4) seedlings. With race 56 good fits were obtained to a ratio of 3 very resistant seedlings: 1 susceptible. That the gene carried by Africa No. 43 is *Sr6* is shown by the results from the cross Africa No. 43 × Red Egyptian. All F_2 plants were very resistant to both races.

Field studies on backcross families confirmed the presence of one gene for resistance to race 15B. Seventeen F_2 families from the backcross to Marquis were tested, and nine segregated for resistance while eight were susceptible. Each family that had segregated in seedling tests also segregated in the field tests. Very few of the backcross plants had good resistance to race 15B and it was evident that plants homozygous for *Sr6* were carrying from 5-30 per cent rust. Fully susceptible plants, however, carried 60-80 per cent rust. Forty-five F_2 families from the backcross to Thatcher were tested in the field with race 15B, and seventeen segregated while twenty-eight were susceptible. The segregation is a satisfactory fit to a 1:1 ratio. A higher degree of resistance was present in plants from the backcrosses to Thatcher than in those from the backcrosses to Marquis, and a good many carried only a trace of rust.

Kenya C9906

Kenya C9906 is very similar in rust resistance to Africa No. 43. Seedlings show a hypersensitive reaction to both races and the mature plants have good resistance to race 15B in the field.

The data from rust tests on the backcross of Kenya C9906 to Marquis are given in Table 4, and the F_2 data from three pertinent crosses are in Table 5. As was the case with Africa No. 43, approximately half the backcross families from Kenya C9906 segregated for a hypersensitive

TABLE 4.—RESULTS OF SEEDLING RUST TESTS ON F_2 FAMILIES FROM THE BACKCROSS OF KENYA C9906 TO MARQUIS

		Race 15B				Totals (race 56)	Expected (1:1)	P
		Number of families						
		Seg. IVR:3S	Seg. 4VR:9MR:3S	Seg. 3MR:1S	S			
Race 56	Seg. 3VR:1S	17	15			32[1]	38	.10–.20
	S			21	23	44	38	
	Totals (race 15B)	17[2]	15[3]	21[4]	23	76	76	
	Expected (1:1:1:1)	19	19	19	19	76		
	P	.50–.70						

The ratios within segregating families were as follows:

Race 56

[1] 480VR:179S plants — P for a 3:1 ratio = .20

Race 15B

[2] 81VR:259S plants — P for a 1:3 ratio = .50–.70

[3] 90VR:188MR:80S plants — P for a 4:9:3 ratio = .10–.20

[4] 396MR:152S plants — P for a 3:1 ratio = .10–.20

TABLE 5.—RESULTS OF RUST TESTS ON F_2 POPULATIONS FROM THE CROSSES OF KENYA C9906 WITH MARQUIS, AFRICA NO. 43 AND RED EGYPTIAN

Cross and type of test	Number of plants				Ratio	P
		VR	MR	S		
Kenya C9906 × Marquis F_2						
Seedling tests —race 56	Observed	106		31		
	Expected	102.75		34.25	3:1	.50–.70
Seedling tests —race 15B	Observed	100		34		
	Expected	108.88		25.13	13:3	.05
Kenya C9906 × Africa No. 43 F_2						
Seedling tests —race 56	Observed	130				
Seedling tests —race 15B	Observed	128				
Field tests —race 15B	Observed	137				
Kenya C9906 × Red Egyptian F_2						
Seedling tests —race 56	Observed	127				
Seedling tests —race 15B	Observed	127				
Field tests —race 15B	Observed	133				

reaction to both race 15B and race 56. The F_2 plants from crosses of Kenya C9906 with Africa No. 43 and Red Egyptian were very resistant to both races. Since Africa No. 43 and Red Egyptian have only gene *Sr6* in common, it is evident that *Sr6* is also present in Kenya C9906.

In addition to *Sr6*, a gene conditioning moderate resistance to race 15B but having no effect on race 56 segregated in approximately half the backcross families. The ratios within segregating backcross families and in the F_2 population from Kenya C9906 × Marquis show that the gene is dominant. Thus in the F_2 population and in backcross families segregating for both *Sr6* and the second gene a ratio of 13 resistant: 3 susceptible seedlings was obtained. The separation of plants carrying the two types of resistance was particularly clear in the backcross families and the segregation gave a good fit to a ratio of 4 very resistant: 9 moderately resistant: 3 susceptible seedlings. In backcross families segregating only for the second gene, a satisfactory fit to a ratio of 3 moderately resistant seedlings: 1 susceptible was found. In expression, this second gene is identical to the gene *Sr7* previously identified by Knott and Anderson (2) in Kenya 58, Kenya 117A and Egypt Na95. Homozygous plants gave a type 1^+ seedling reaction to race 15B, while heterozygotes went as high as type 3. All resistant seedlings showed a typical yellowing around the pustules. Results to be reported in a later paper show that the cross Kenya 117A × Kenya C9906 does not segregate for resistance to race 15B. Since *Sr7* is the only gene for resistance to race 15B carried by Kenya 117A, Kenya C9906 must also carry *Sr7*.

Seventeen F_2 families from the backcross of Kenya C9906 to Marquis were tested in the field with race 15B. The families which had segregated for a hypersensitive seedling reaction segregated for good resistance in the field. However, the families which segregated for moderate seedling resistance showed very little resistance in the field. Apparently, in this particular cross *Sr7* conditions a poor type of field resistance.

Forty F_2 families from a backcross of Kenya C9906 to Thatcher were tested in the field. Four types of families appeared. In one group of twelve segregating families approximately three-quarters of the plants carried 0-10 per cent rust. In a second group of twelve segregating families less than half of the plants carried 0-10 per cent rust. A third group of seven families segregated for resistance, but almost no plants carried less than 5 per cent rust. Finally, nine families were susceptible. The segregation, 12: 12: 7: 9, is a good fit to a 1: 1: 1: 1 ratio. Apparently, the first group of families were segregating for both *Sr6* and *Sr7*, the second group only for *Sr6*, the third group only for *Sr7* and the last group for neither. Contrary to the results with the Marquis backcrosses, it was evident that in the Thatcher backcrosses *Sr7* conditioned moderate resistance to race 15B in the field.

Kenya 338.AC.2.E.2

Kenya 338.AC.2.E.2 seedlings exhibit a type 1^-—1 reaction to race 15B and a fleck to type 1^- reaction to race 56. Plants grown in the field have excellent resistance to race 15B.

The cross Kenya 338.AC.2.E.2 × Marquis resulted in plants that were sterile dwarfs and no backcrosses were possible. In addition, the crosses

TABLE 6.—RESULTS OF RUST TESTS ON F_2 POPULATIONS FROM THE CROSSES OF KENYA 338.AC.2.E.2 WITH THATCHER, AFRICA NO. 43 AND KENYA C9906

Cross and type of test		Number of plants			Ratio	P
		VR	MR	S		
Kenya 338.AC.2.E.2 × Thatcher F_2						
Seedling tests —race 56	Observed	128		9	15:1	1.0
	Expected	128.4		8.6		
Seedling tests —race 15B	Observed	99		33	3:1	1.0
	Expected	99		33		
Kenya 338.AC.2.E.2 × Kenya C9906 F_2						
Seedling tests —race 56	Observed	97	36	3	48:15:1	.50–.70
	Expected	102.0	31.9	2.1		
Seedling tests —race 15B	Observed	98		0		
Field tests —race 15B	Observed	172		0		
Kenya 338.AC.2.E.2 × Africa No. 43 F_2						
Seedling tests —race 56	Observed	69	20	1	48:15:1	.90–.95
	Expected	67.5	21.1	1.4		
Seedling tests —race 15B	Observed	55		1	15:1	.10–.20
	Expected	52.3		3.7		

of Kenya 338.AC.2.E.2 with Red Egyptian, P.I. 170910 and Na101 produced sterile dwarfs and the cross Kenya 338 × Africa No. 43 gave dwarf plants which yielded only a few seeds. However, the manner of inheritance of rust resistance in Kenya 338 was determined from the remaining diallel crosses. The results are given in Table 6.

The clearest F_2 data came from the cross Kenya 338.AC.2.E.2.× Thatcher. Thatcher resistance to race 56 can be ignored, since at least two complementary recessive genes are involved and they will have little effect on the ratio obtained. When tested with race 56, the F_2 population segregated to give 128 resistant seedlings: 9 susceptible, a very good fit to a 15: 1 ratio. With race 15B the segregation was 99 resistant: 33 susceptible, a perfect fit to a 3:1 ratio. The data indicate that Kenya 338.AC.2.E.2 carries one dominant gene for resistance to race 15B and two dominant genes for resistance to race 56.

The gene for resistance to race 15B in Kenya 338.AC.2.E.2 is identical in expression to the gene *Sr7* carried by Kenya C9906. The cross between the two varieties did not segregate for resistance to race 15B, proving that the gene is *Sr7*. When tested with race 56 the same cross segregated in a ratio of 48 very resistant seedlings (fleck to type 1^-): 15 resistant: 1 susceptible. This is the ratio expected assuming that two genes from Kenya 338.AC.2.E.2 were present in addition to *Sr6*, which conditions resistance to race 56 in Kenya C9906.

The two genes for resistance to race 56 in Kenya 338.AC.2.E.2 condition types of resistance that are very similar to the resistances given by the genes *Sr9* and *Sr10* which Knott and Anderson reported in Kenya 117A

and Egypt Na95. In a later paper data will be presented from a cross between Kenya 338.AC.2.E.2 and Kenya 117A which shows that the two varieties have at least one, and very probably both genes in common.

The data obtained from the cross Kenya 338.AC.2.E.2 × Africa No. 43 are in agreement with the genotypes hypothesized for the two varieties. For resistance to race 56 three dominant genes, *Sr6* from Africa No. 43 and presumably *Sr9* and *Sr10* from Kenya 338.AC.2.E.2, were segregating and a good fit to a ratio of 48 very resistant seedlings: 15 moderately resistant: 1 susceptible was obtained. For resistance to race 15B two genes, *Sr6* from Africa No. 43 and *Sr7* from Kenya 338.AC.2.E.2 were segregating and the results give a satisfactory fit to a ratio of 15 resistant seedlings: 1 susceptible.

Forty-seven families from the backcross of Kenya 338.AC.2.E.2 to Thatcher were tested for field resistance to race 15B. Twenty-four, or approximately half the families segregated for resistance, indicating the presence of one gene. The segregating families were of two types. In one group of thirteen families, approximately three-fourths of the plants carried 10 per cent or less rust. In the remaining eleven families, fewer than one-half the plants carried 10 per cent or less rust. Apparently one major modifier of resistance is present.

Egypt Na101 (Kenya Governor)

Seedlings of Egypt Na101 give a 3^+ reaction to race 56 and a 1^+ reaction to race 15B. In the field the variety is resistant to race 15B but most plants carry some rust. A few of the plants used as parents in this study segregated for rust reaction.

The inheritance of rust resistance in Egypt Na101 proved to be very simple. The results of rust tests on F_2 families from the backcross to Marquis are given in Table 7. When tested with race 15B, approximately half the backcross families segregated 3 moderately resistant seedlings: 1 susceptible. Although the classification of each family was clear-cut the separation between moderately resistant and susceptible plants within families was not always distinct. The data show, however, that Egypt Na101 carries one gene for resistance to race 15B.

TABLE 7.—RESULTS OF RUST TESTS ON F_2 FAMILIES FROM THE BACKCROSS OF EGYPT NA101 TO MARQUIS

		Race 15B		Totals
		Number of families		
		Seg. 3MR:1S	S	
Race 56	S	43	34	77
Totals (race 15B)		43[1]	34	77
Expected (1:1)		38.5	38.5	77
P		.30–.50		

[1] The ratio within segregating families was 636 MR:240 S plants P for a 3:1 ratio = .10–.20

The gene in Egypt Na101 conditions the type of reaction typical of gene *Sr7*, that is a large type 1 pustule surrounded by a yellow chlorotic area. Unfortunately, the cross Egypt Na101 × Kenya 338 AC.2.E.2 gave only sterile dwarfs and the cross Egypt Na101 × Kenya C9906 was one in which the Egypt Na101 parent was heterozygous for resistance. Some of the F_2 families from the latter cross segregated for only the two genes from Kenya C9906, while others were resistant to race 15B. The resistant families are undoubtedly the true ones and Egypt Na101 must, therefore, carry *Sr7*.

The crosses Egypt Na101 × Africa No. 43 and Egypt Na101 × Red Egyptian segregated as expected when tested with race 15B. The data are given in Table 8. In the first cross each variety contributed one dominant gene for resistance and a satisfactory fit to a ratio of 12 very resistant seedlings: 3 moderately resistant: 1 susceptible was obtained. In the second cross Red Egyptian contributed two dominant genes and Egypt Na101 contributed one. The segregation obtained was a good fit to a ratio of 48 very resistant seedlings: 15 moderately resistant: 1 susceptible. In the F_2 populations from crosses of Egypt Na101 with Marquis and Thatcher the separation of plants into classes was not certain and the data are not reported.

Thirty-four F_2 families from the backcross of Egypt Na101 to Thatcher were tested in the field with race 15B. Twenty families segregated for resistance, but only a few plants in each carried a low percentage of rust. The F_1 plants from the backcross had been tested with race 15B as seedlings and, as expected, each resistant F_1 plant produced a segregating progeny. A few F_1 plants were apparently misclassified as susceptible since their progenies segregated for resistance.

Thirty-seven F_2 families from the backcross of Egypt Na101 to Marquis were tested in the field with race 15B. It proved to be impossible to separate the segregating from the susceptible families. The most resistant plants carried 20 per cent rust while few of the susceptible ones carried more than 50 per cent. Seedlings from each of the thirty-seven families had previously been tested with race 15B and in general families which segregated for seedling resistance carried a little less rust than families which were susceptible.

TABLE 8.—RESULTS OF RUST TESTS ON F_2 POPULATIONS FROM THE CROSSES OF EGYPT NA101 WITH AFRICA NO. 43 AND RED EGYPTIAN

Cross and type of test		Number of plants			Ratio	P
		VR	MR	S		
Egypt Na101 × Africa No. 43 F_2						
Seedling tests —race 15B	Observed	91	33	7	12:3:1	.10–.20
	Expected	98.2	24.6	8.2		
Egypt Na101 × Red Egyptian F_2						
Seedling tests —race 15B	Observed	90	30	3	48:15:1	.50–.70
	Expected	92.3	28.8	1.9		

Veadeiro

Veadeiro has good resistance to race 56 in the seedling stage and gives a type 1^{-}—1 reaction. The seedlings, however, have little resistance to race 15B and give a type 3—3^{+} reaction. In the field Veadeiro shows fairly good resistance to race 15B and usually carries less than 5 per cent rust. The original stock of the variety used in this study was variable for a number of characters including rust resistance and selections had to be made from it.

The results of rust tests on the backcross of Veadeiro to Marquis are given in Table 9. In seedling tests all of the backcross families were susceptible to race 15B, although a few plants were classified as having a type 3 reaction rather than a type 4. Approximately three-quarters of the families segregated for resistance to race 56, indicating that Veadeiro probably carries two genes. One gene conditions a type 2 reaction and the second a type 2^{+}—3^{-}. In some families, presumably those segregating for the second gene, the separation of resistant and susceptible plants was difficult and no attempt was made to determine ratios within families. Where segregation was clearcut good 3:1 ratios were obtained in some cases and 15:1 ratios in others. None of the plants in the segregating families was as resistant as Veadeiro itself.

The data from tests with race 56 on F_2 populations from some of the crosses involving Veadeiro are given in Table 10. The separation of resistant and susceptible plants was difficult in crosses involving Thatcher and Egypt Na101, and no attempt was made to fit the results to ratios. In the cross Veadeiro × Marquis classification was reasonably good and the data give a satisfactory fit to a ratio of 15 moderately resistant seedlings: 1 susceptible. A clear separation was apparent in the cross Veadeiro × Africa No. 43. Africa No. 43 carries a single dominant gene conditioning a hypersensitive type of reaction to race 56, and, if it is assumed that Veadeiro has two partially dominant genes, the expected ratio from the cross is 48 very resistant seedlings: 15 moderately resistant: 1 susceptible. The observed segregation is an excellent fit to this ratio. A similar result should have been obtained in the cross with Kenya C9906. The segregation was not a good fit to a 48:15:1 ratio due to an excess of susceptible plants contributed by two of five families tested.

TABLE 9.—RESULTS OF SEEDLING RUST TESTS ON F_2 FAMILIES FROM THE BACKCROSS OF VEADEIRO TO MARQUIS

		Race 15B	Expected (3:1)	P
		Number of families		
		S		
Race 56	Seg.	68	76.5	.05–.10
	S.	34	25.5	
Totals		102	102	

TABLE 10. RESULTS OF SEEDLING RUST TESTS WITH RACE 56 ON POPULATIONS FROM THE CROSSES OF VEADEIRO WITH MARQUIS. AFRICA NO. 43, KENYA C9906, KENYA 338.AC.2.E.2, RED EGYPTIAN AND P.I. 170910.

Cross		Number of plants			Ratio	P
		VR	MR	S		
Veadeiro × Marquis	Observed		112	12		
	Expected		116.2	7.8	15:1	.10–.20
Veadeiro × Africa No. 43	Observed	81	22	2		
	Expected	78.8	24.6	1.6	48:15:1	.80–.90
Veadeiro × Kenya C9906	Observed	100	25	6[1]		
	Expected	98.3	30.7	2.0	48:15:1	.01–.02
Veadeiro × Kenya 338.AC.2.E.2	Observed	127				
Veadeiro × Red Egyptian	Observed	106	34			
	Expected	105	35		3:1	.80–.90

[1] All of the susceptible plants were contributed by two of five families tested.

The cross Veadeiro × Kenya 338.AC.2.E.2. gave interesting results. All 127 plants tested were as resistant to race 56 as the parents, that is they gave a type 1⁻—1 reaction. Since none of the genes in the two varieties conditions better than a 2 reaction when alone, it appears probable that Veadeiro and Kenya 338.AC.2.E.2. carry the same two genes for resistance to race 56. If only one gene were common to the two varieties, some F_2 segregates should have given a type 2 reaction. The two genes in Veadeiro are, therefore, presumed to be *Sr9* and *Sr10*, although no direct proof of this is available. Further evidence that Veadeiro carries *Sr9* comes from the cross with Red Egyptian. All of the F_2 seedlings showed either the hypersensitive reaction conditioned by *Sr6* (from Red Egyptian) or the moderate resistance conditioned by *Sr9* and *Sr10*.

The inheritance of mature plant resistance to race 15B in Veadeiro was determined in field tests of F_2 families from backcrosses to Thatcher and Marquis. Of forty-seven backcrosses to Thatcher which were tested, thirty-four appeared to segregate. In a few cases it was difficult to be sure that families were segregating; however, it seems probable that Veadeiro carries two genes for resistance. In thirteen of the families, at least one-third of the plants were resistant and some showed only a trace of rust. These presumably were the families segregating for both genes. The rest of the segregating families had fewer resistant plants and the best ones carried 5-10 per cent rust.

The backcrosses of Veadeiro to Marquis were much less resistant than the comparable backcrosses to Thatcher and, consequently, were more difficult to classify. Of twenty-one families tested, four had some plants with less than 10 per cent rust, while in twelve, the best plants carried 10-30 per cent rust. The remaining five had no plants with less than 40 per cent rust. While the separation was not absolutely clear, the results, coupled with those from the Thatcher backcrosses, suggest that Veadeiro

carries two additive genes for mature plant resistance to race 15B. Symbols will not be assigned to these genes until additional genetic data have been obtained.

P.I. 170910 (Red Egyptian type)

Seedlings of P.I. 170910 exhibit a hypersensitive reaction to races 15B and 56 and the plants are highly resistant to race 15B in the field. It was expected from the name used for this variety that it was a Red Egyptian cross and might, therefore, carry the same genes for rust resistance as Red Egyptian. This proved to be the case.

The data on the backcrosses of P.I. 170910 to Marquis are given in Table 11. The results show that the variety carries one gene conditioning a high degree of resistance to both races, a second gene conditioning moderate resistance to both races and a third gene conditioning moderate resistance to race 56. In their expression these three genes are very similar to the genes *Sr6*, *Sr8* and *Sr9* carried by Red Egyptian and, as is shown below, there is little doubt that they are the same. The first gene, *Sr6*, conditions a hypersensitive reaction to both races but is recessive with

TABLE 11.—RESULTS OF SEEDLING RUST TESTS ON F_2 FAMILIES FROM THE BACKCROSS OF P.I. 170910 TO MARQUIS

		Race 15B				Totals (race 56)	Expected (1:1:1:1: 1:1:1:1)	P
		Number of families						
		Seg. 1VR:3S	Seg. 4VR:12MR-S	Seg. MR-S	Susc.			
Race 56	Seg. 3VR:1S	7				7[1]	8.6	.90–.95
	Seg. 12VR:3MR:1S	9				9[2]	8.6	
	Seg. 12VR:4MR-S		7			7[3]	8.6	
	Seg. 48VR:15MR:1S		10			10[4]	8.6	
	Seg. MR-S			7		7[5]	8.6	
	Seg. 15MR:1S			9		9[6]	8.6	
	Seg. 3MR:1S				12	12[7]	8.6	
	Susc.				8	8	8.6	
	Totals (race 15B)	16[8]	17[9]	16[10]	20	69	69	
	Expected (1:1:1:1)	17.2	17.2	17.2	17.2	69		
	P	.80–.90						

The ratios within segregating families were as follows:

Race 56

[1] 114VR:50S plants — P for a 3:1 ratio = .10–.20
[2] 126VR:38MR:16S plants — P for a 12:3:1 ratio = .20–.30
[3] 129VR:47MR-S plants — P for a 12:4 ratio = .50–.70
[4] 213VR:75MR:7S plants — P for a 48:15:1 ratio = .30–.50
[5] No clear separation into classes was possible
[6] 174MR:12S plants — P for a 15:1 ratio = 1.0
[7] 318MR:103S plants — P for a 3:1 ratio = .80–.90

Race 15B

[8] 112VR:308S plants — P for a 1:3 ratio = .30–.50
[9] 115VR:397MR-S plants — P for a 4:12 ratio = .10–.20
[10] No clear separation into classes was possible.

race 15B and dominant with race 56. Both of the other genes are partially dominant. The second, *Sr8*, conditions a type 2—2^+ reaction to both races with the resistance being a little better to race 56 than to race 15B. The third, *Sr9*, conditions a type 2—2^+ reaction to race 56. In the backcrosses to Marquis the segregations for *Sr6* and *Sr9* were clearcut. For

TABLE 12.—RESULTS OF RUST TESTS ON F_2 POPULATIONS FROM THE CROSSES OF P.I. 170910 WITH MARQUIS, THATCHER, EGYPT NA101, AFRICA NO. 43, KENYA C9906, RED EGYPTIAN AND VEADEIRO

Cross and type of test		Number of plants			Ratio	P
		VR	MR	S		
P.I. 170910 × Marquis F_2						
Seedling tests —race 56	Observed	105	40	4	48:15:1	.20–.30
	Expected	111.8	34.8	2.3		
P.I. 170910 × Thatcher F_2						
Seedling tests —race 56	Observed	110	33	2	48:15:1	.80–.90
	Expected	108.7	34.0	2.3		
P.I. 170910 × Egypt Na101 F_2						
Seedling tests —race 56	Observed	106	32	1	48:15:1	.70–.80
	Expected	104.2	32.6	2.2		
Seedling tests —race 15B	Observed	116		3	63:1	.30–.50
	Expected	117.1		1.9		
P.I. 170910 × Africa No. 43 F_2						
Seedling tests —race 56	Observed	137				
Seedling tests —race 15B	Observed	88				
Field tests —race 15B	Observed	132				
P.I. 170910 × Kenya C9906 F_2						
Seedling tests —race 56	Observed	143				
Seedling tests —race 15B	Observed	125				
Field tests —race 15B	Observed	114				
P.I. 170910 × Red Egyptian F_2						
Seedling tests —race 56	Observed	129				
Seedling tests —race 15B	Observed	146				
Field tests —race 15B	Observed	163				
P.I. 170910 × Veadeiro F_2						
Seedling tests —race 56	Observed	109	22		3:1	.02–.05
	Expected	98.2	32.8			

Sr8, however, there was some difficulty in determining which seedlings were heterozygous and which susceptible. As a result some of the segregations involving *Sr8* could not be fitted to ratios. When both *Sr8* and *Sr9* were segregating the separation of the seedlings into classes was more distinct and good fits to the expected ratios were obtained.

The results from some of the tests on F_2 populations from crosses involving P.I. 170910 are given in Table 12. The data on the crosses with Marquis, Thatcher and Egypt Na101 confirm that P.I. 170910 carries three genes for resistance to race 56. Since Marquis and Egypt Na101 are susceptible to race 56 and the inheritance of the resistance from Thatcher can be assumed to have a negligible effect, the expected ratio for each cross is 48 very resistant seedlings: 15 moderately resistant: 1 susceptible. All three segregations are good fits to this ratio. Proof that P.I. 170910 carries *Sr6* comes from the crosses with the three varieties, Africa No. 43, Kenya C9906 and Red Egyptian, which have been shown to have *Sr6*. The F_2 plants from the three crosses were very resistant to both race 15B and 56. Since Veadeiro carries *Sr9* it was expected that the cross between it and P.I. 170910 would not segregate for resistance to race 56. This proved to be true, although the observed frequency of very resistant and moderately resistant plants was not a good fit to the expected 3:1 ratio. The discrepancy is probably due either to poor classification or to chance.

No direct proof is available that the gene in P.I. 170910 which conditions moderate resistance to both races is *Sr8*. The presumptive evidence is, however, strong.

TABLE 13.—PROBABLE GENOTYPE OF EACH VARIETY. (THE VARIETIES DESCRIBED BY KNOTT AND ANDERSON (2) ARE GIVEN IN THE SECOND PART OF THE TABLE)

Variety	Genotype						
Africa No. 43	*Sr6Sr6*						
Kenya C9906	*Sr6Sr6*	*Sr7Sr7*					
Kenya 338.AC.2.E.2		*Sr7Sr7*		*Sr9Sr9*	*Sr10Sr10*		
Egypt Na101		*Sr7Sr7*					
Veadeiro[1]				*Sr9Sr9*	*Sr10Sr10*		
P.I. 170910	*Sr6Sr6*		*Sr8Sr8*	*Sr9Sr9*			
Kenya 58	*Sr6Sr6*	*Sr7Sr7*					
Red Egyptian	*Sr6Sr6*		*Sr8Sr8*	*Sr9Sr9*			
Kenya 117A		*Sr7Sr7*		*Sr9Sr9*	*Sr10Sr10*		
Egypt Na95		*Sr7Sr7*		*Sr9Sr9*	*Sr10Sr10*		
McMurachy	*Sr6Sr6*						
Gabo						*Sr11Sr11*	*Sr12Sr12*
Lee						*Sr11Sr11*	*Sr12Sr12*
Timstein						*Sr11Sr11*	*Sr12Sr12*

[1] Veadeiro probably carries two additional genes for mature plant resistance to race 15B.

DISCUSSION

The probable genotype of each variety described in this paper and in the previous paper by Knott and Anderson (2) is given in Table 13.

One of the surprising features of the work is the paucity of genes for resistance to races 15B and 56 despite the diverse origins of the varieties studied. Except for Veadeiro, all of the varieties in this second group carried various combinations of the genes already reported in the first group of varieties.

At the present time plant breeders are particularly interested in resistance to race 15B. Three genes for resistance to race 15B have been definitely reported, of which probably only two, *Sr6* and *Sr7*, are useful in plant breeding. The third gene, *Sr8*, is of little value alone, but may have an additive effect on resistance in combination with other genes. The resistance to race 15B carried by Veadeiro is of the mature plant type and appears to be conditioned by two additive genes. As far as is known, the resistance of Veadeiro is not being exploited in wheat breeding except at the University of Saskatchewan.

The importance of modifiers or, perhaps, of a genic environment on rust resistance is again emphasized in the present work. While the genes reported determine whether a variety is or is not resistant to races 15B and 56, the degree of resistance they condition is variable in different crosses. For several varieties (e.g., Veadeiro and Egypt Na101) it was noted that segregates from crosses with Marquis were considerably less resistant in the field than corresponding segregates from crosses with Thatcher. In these cases it is not known whether the difference is due to specific modifiers carried by Thatcher or to the genic environment in general. In Kenya 338. AC. 2.E.2 it is clear that there is one main modifier of the resistance to race 15B conditioned by *Sr7*. Evidence presented by Knott and Anderson (2) indicated that in Kenya 117A and Egypt Na95 either one or both of *Sr9* and *Sr10* acted as modifiers of the gene *Sr7*.

This "modifier effect" probably explains many of the difficulties encountered in maintaining full resistance while backcrossing to produce rust resistant varieties.

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EFFECT OF MOLYBDENUM APPLICATIONS ON LEGUMINOUS HAY CROPS IN PRINCE EDWARD ISLAND[1]

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ABSTRACT

Seed treatments of molybdenum were found to increase yields of early red clover on three soil types in Prince Edward Island. Plots receiving 8 or more ounces of molybdenum per acre were significantly better than the control plots. Applications of 1000 lb. and 2000 lb. of ground limestone per acre had no effect on the yields of molybdenum-treated clover but the uptake of molybdenum by plants was highest where the 2000 lb.-per-acre rate was applied. The influence of added molybdenum on clover root nodule formation was determined on one soil type. Eight ounces of molybdenum per acre gave a significant increase in the weight of root nodules on the treated plants.

Molybdenum is an important micronutrient for many forage legumes, and marked increases in yields of hay and pasture have been obtained in Australia, New Zealand and the Netherlands by field applications of molybdates (1, 4, 5). This response of legumes occurs, in part, because molybdenum is required in symbiotic nitrogen fixation (2, 5). Molybdenum applications have increased yields of hay on some acidic sandy-loam soils in Prince Edward Island.

An experiment was carried out at four locations representative of three soil types. There were three treatments of early red clover seed

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TABLE 1.—THE EFFECT OF ADDED MOLYBDENUM ON THE YIELD OF A GRASS-LEGUME SEED MIXTURE WITH AND WITHOUT INOCULATION WITH NITROGEN-FIXING BACTERIA

Seed treatment	Mean yields of green hay in pounds per plot			
	Location and type of soil			
	Charlottetown sandy loam pH 5.32	Hunter River sandy loam pH 5.68	Alliston fine sandy loam pH 5.91	O'Leary sandy loam to loam pH 5.89
Control—no treatment	11.0	11.7	36.5	35.4
(a) Molybdenum added at 8 oz. per ac.	21.7	18.5	35.9	49.2
(b) Inoculated with *Rhizobia* spp.	13.7	13.0	40.0	39.9
(c) Inoculated, plus added molybdenum at 8 oz. per ac.	19.1	26.3	39.0	47.4
L.S.D. at P = 0.05	4.6	5.3	—	6.2

at each location: (a) molybdenum at 8 oz. per acre applied to the seed as sodium molybdate; (b) seed inoculated with commercial cultures of *Rhizobia* spp. to supply essential nitrogen-fixing bacteria, and (c) a combination of (a) and (b). Control plots were sown with untreated seed. Results are shown in Table 1.

At three of the four locations, the plots that received treatment (a) gave significantly greater yields than the plots receiving treatment (b). Plots sown with inoculated and molybdenum-treated seed (c) gave yields not significantly different from plots that received molybdenum alone (a), except in the case of the Hunter River location.

The influence of added molybdenum on root nodule formation was determined at one location. Nodules were collected to a depth of 6 inches from ten plants per plot. In comparison with the control and with inoculation alone, the application of molybdenum resulted in a significantly greater weight of nodules, as shown in Table 2.

TABLE 2.—THE EFFECT OF ADDED MOLYBDENUM AND OF SEED INOCULATION WITH NITROGEN-FIXING BACTERIA ON NODULE FORMATION IN RED CLOVER

Seed treatment	Mean nodule weight* (mg. oven-dried)
Control—no treatment	31.8
(a) Molybdenum added at 8 oz. per acre	51.3
(b) Inoculated with *Rhizobia* supp.	38.3
(c) Inoculated, plus added molybdenum at 8 oz. per acre	54.7
L.S.D. at P = 0.05	13.3

* Nodules collected to a depth of 6 inches.

Work by others (4, 7) has indicated that liming increases the availability of any molybdenum that may be present in the soil. An experiment to study lime-molybdenum interaction was carried out. Ground limestone at 0, 1000 lb. and 2000 lb. per acre, and molybdenum at 0, 5 oz., 10 oz. and 15 oz. per acre, were applied in all combinations to plots in an area having an initial pH of 5.3. Early red clover was seeded in pure stand as a test crop. The molybdenum was applied to the seed as ammonium molybdate. Table 3 shows the yield and molybdenum content of red clover from the various treatments.

These results indicate the potential value of molybdenum for increasing yields of red clover hay in acid, leached soils. While there was no significant interaction of ground limestone and molybdenum, it is apparent that the uptake of the element by the plants was greater where the higher rates of ground limestone were applied. This is in agreement with the findings of New Zealand workers (7) and suggests that care should be

FIGURE 1.—The effect of molybdenum on the growth of a legume hay crop.
Left—No molybdenum was applied.
Right—Molybdenum in the form of ammonium molybdate was applied at 4 oz. per acre as a spray in early spring.

TABLE 3.—THE EFFECT OF GROUND LIMESTONE AND MOLYBDENUM APPLICATIONS ON THE YIELD AND MOLYBDENUM CONTENT OF RED CLOVER

Molybdenum applied (oz. per ac.)	Ground limestone applied (lb. per acre)						Mean yield
	0		1000 lb.		2000 lb.		
	Yield[1]	Mo content[2] p.p.m.	Yield[1]	Mo content[2] p.p.m.	Yield[1]	Mo content[2] p.p.m.	
0	488.8	0.97	492.7	1.00	440.1	1.10	473.9
5	549.9	1.63	544.8	2.62	409.4	2.19	501.3
10	680.9	2.25	583.5	4.02	504.3	5.81	589.6
15	546.8	2.88	456.0	4.72	534.8	6.51	512.5
	L.S.D. for molybdenum applications at P = 0.05						78.4

(1) Yield is expressed as average pounds of dry matter per acre.

(2) Molybdenum content is given as the average p.p.m. of two samples from each treatment on a dry matter basis.

taken in applying molybdenum to heavily limed soils in order to avoid molybdenosis to cattle feeding on the forage. Kline (6) gives 10 parts per million of molybdenum in dry herbage as the potentially dangerous level. Cunningham *et al.* (3) indicate that 3 parts per million in pasture herbage may be too high if the copper content is low. Molybdenum content of the herbage samples was determined by an adaptation of the method described by Ward and Johnston (8). Figure 1 illustrates an application of 4 oz. per acre of molybdenum to an early red clover-timothy mixture growing on Charlottetown sandy loam. This treatment was applied in the form of an ammonium molybdate spray in early spring. The increased growth of red clover on the treated plots is very apparent.

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EFFECT OF INSECTICIDES AND HERBICIDES APPLIED TO SOIL ON THE DEVELOPMENT OF PLANT DISEASES. I. THE SEEDLING DISEASE OF BARLEY CAUSED BY *HELMINTHOSPORIUM SATIVUM* P. K. & B.[1]

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ABSTRACT

From the results obtained when nine insecticides and ten herbicides were applied at a series of dosages to soil infested to various degrees with *Helminthosporium sativum* P.K. & B. it was found possible to separate these chemicals into four groups on the basis of their effects on the growth of barley seedlings and on the development of rootrot infection. Group A (schradan, isodrin, DCU, IPX, and TCA) affected neither host nor disease development. Group B (lindane, dieldrin, and DDT) stimulated the growth of barley seedlings without affecting disease development. Group C (maleic hydrazide and heptachlor) stimulated seedling growth but increased the severity of infection. Group D (aldrin, endrin, chlordane, NPA, 2,4-D, monuron, DNBP, and dalapon) did not affect the growth of seedlings but reduced rootrot infection. Only DNBP was toxic to *H. sativum* in culture.

INTRODUCTION

Many agricultural chemicals used for insect and weed control find their way into the soil either through direct application or through accumulation of debris from sprayed plants. A knowledge of the effects of these materials on soil micro-organisms, both parasites and saprophytes, is obviously desirable but difficult to achieve because of the complexity of the problem and the limitations of available techniques. Since the pertinent literature is scattered in various journals, many of which are not devoted to plant pathology, it seems advisable to present a brief review at this point.

Changes in the population of soil micro-organisms following applications of insecticides and herbicides have been observed by many workers. The effects of these chemicals on bacterial populations have been studied principally in relation to soil fertility and therefore will not be discussed here. Their effect on the fungal populations may have some significance in relation to disease development. A decrease in the numbers of soil fungi has been reported following the application of BHC (2,23), chlordane (23), DDT (2) and aldrin (2). Increased numbers of fungi were found after treatment with toxaphene (2,23). 2,4-D applied at normal rates for killing plants was reported to have no appreciable effect on the soil fungi (14,22).

The effects of insecticides and herbicides on the germination and growth of fungi in culture have also been studied. Parathion and related organophosphorus compounds were found to inhibit the germination of

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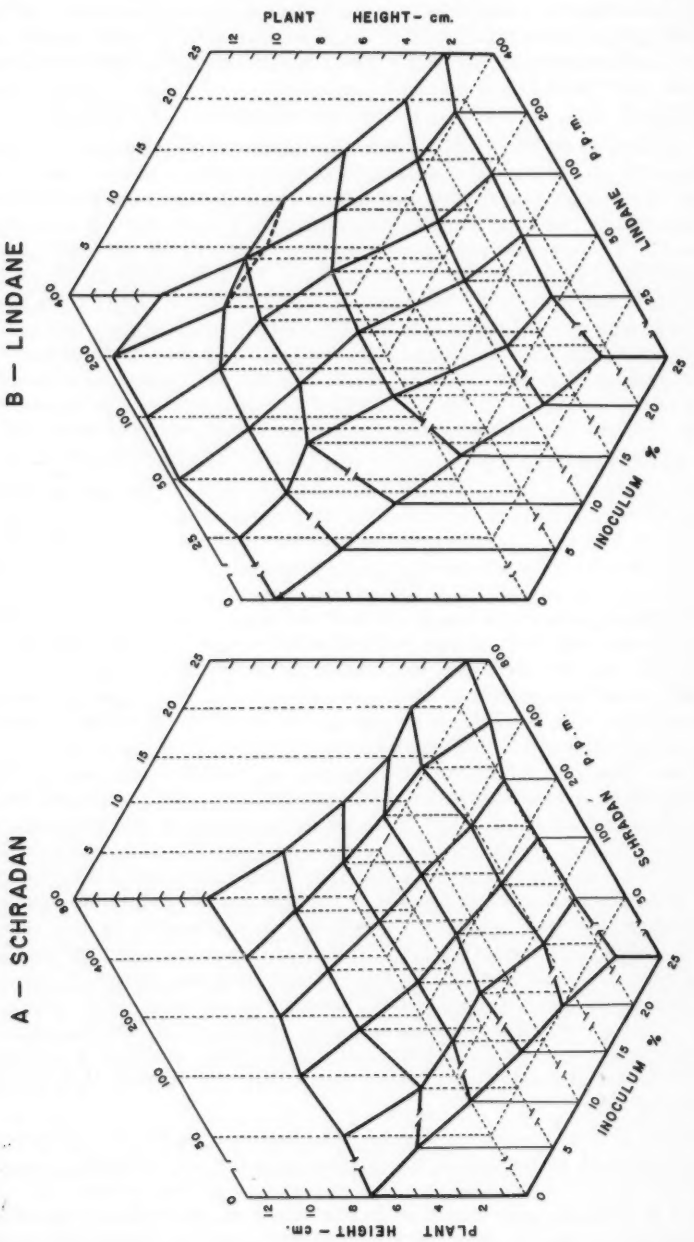
spores of *Venturia inaequalis* and *V. pyrina* while schradan did not have this fungistatic effect (13). The delta isomer of BHC was found to be toxic to *Rhizoctonia solani* (27). The reported effects of 2,4-D on fungi in culture vary from fungitoxic and fungistatic to stimulatory, depending on the formulation, concentration and test organism (1,7,8,9,19,24).

Several cases have been reported where the development of fungus diseases of plants has been affected by insecticides. Khapli wheat seedlings, for example, became susceptible to races of stem rust to which they were normally resistant when sprayed with DDT a few days prior to inoculation. This response was specific to the variety, and the pathogenicity of the rust races involved was not changed (12, 10). High concentrations of DDT in soil apparently rendered seedlings of many plants more susceptible to damping-off fungi whereas BHC and chlordane appeared to inhibit these pathogens (4). DDT and BHC preparations showed some fungicidal value against *Puccinia antirrhini* when applied with spores of this rust to snapdragon leaves (6). Systox applied to sugar-beets as a prophylactic spray reduced the incidence of infection by *Cercosporella beticola* (26).

The herbicides found to affect disease development have been of the growth-regulating type. 2,4-D was found to inhibit the germination of urediospores and growth of germ tubes of *Puccinia graminis avenae*. When applied to leaves it also reduced the number of uredia on a susceptible oat variety but the characteristic varietal reactions to stem-rust races were not altered significantly (11). High concentrations of 2,4-D were required to inhibit germination of urediospores of *Puccinia coronata* (18). Wheat seedlings sprayed with maleic hydrazide had larger leaf rust pustules (15) and were consistently more susceptible to stem rust (3) than untreated plants. Immune reactions were not altered, however, and a resistant type reaction did not change to susceptible except in the variety Khapli. The pathogenicity of *Helminthosporium sativum* to Mida wheat was increased when the inoculum was grown on medium containing 2,4-D. This result was evidently due to the predisposing effect of 2,4-D on the host plant rather than to an increase in virulence of the pathogen (9). 2,4-D and other growth-regulators did not alter the normal reaction of Red Kidney and Kentucky Wonder beans to alpha and beta strains of *Colletotrichum lindemuthianum* (17). There was some reduction of severity of infection, however, which was attributed to suppression of development of susceptible host tissues by 2,4-D rather than a modification of the plant metabolism. 2,4-D applied to flax foliage had no apparent effect on its reaction to pasmo, rust, authracnose, or stem break (20). Spraying tomato foliage with 2,4-D and other plant growth regulators was found to increase resistance to Fusarium wilt (5). Plants sprayed with maleic hydrazide, on the other hand, were more severely affected by *Fusarium lycopersici* (25).

With a view to gaining further information concerning the effect of insecticides and herbicides on the development of plant diseases of various types, a series of investigations was undertaken at this laboratory. The present communication deals with the effect of such chemicals on the development of the seedling disease of barley caused by *Helminthosporium sativum* P.K. & B.


PLANT HEIGHT – cm.
B – LINDANE
LINDANE P.P.M.
INOCULUM %
A – SCHRADAN
SCHRADAN P.P.M.
INOCULUM %
PLANT HEIGHT – cm.

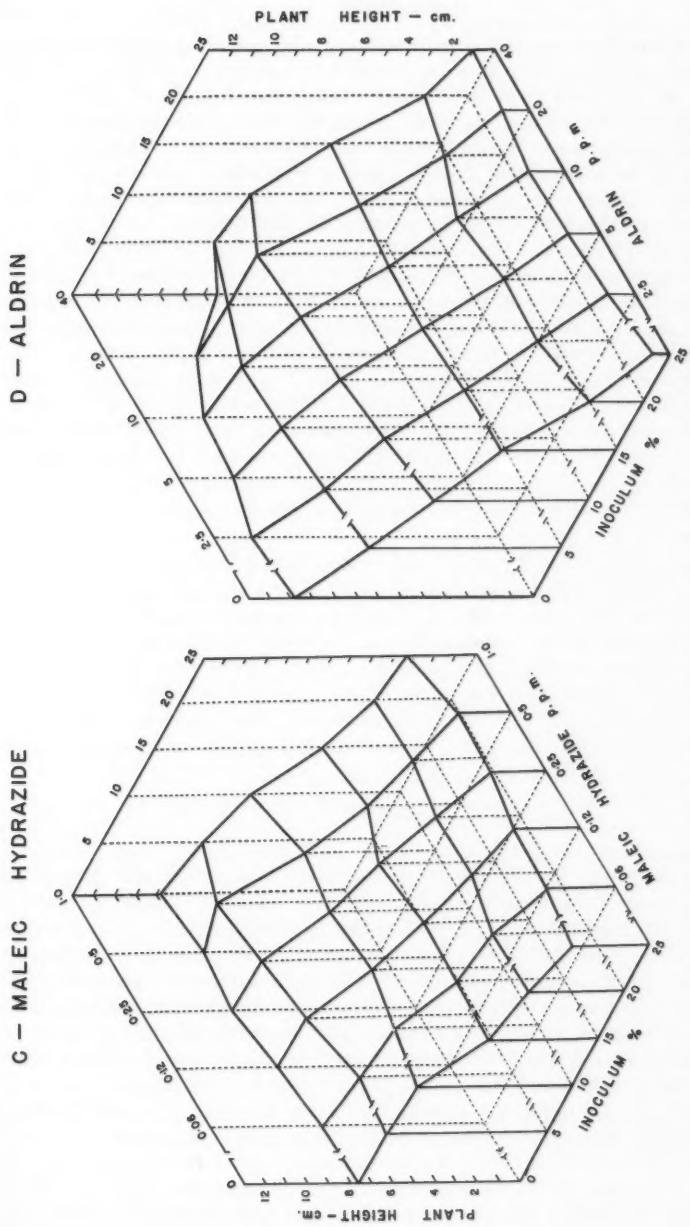


FIGURE 1. The effect of insecticides and herbicides applied to soils infested with *Helminthosporium sativum* on the height of barley seedlings. The examples are representative of four groups of chemicals separated on the basis of their effect on host and disease development (see Table I and text).

METHODS

The techniques employed in producing and assessing Helminthosporium rootrot infection were those developed by Ludwig *et al.* (16). Barley seedlings were grown in a light sandy soil infested with *H. sativum* to various degrees by mixing different proportions of inoculum grown on a sand-cornmeal mixture fortified with Czapek's medium. The chemicals were applied in a logarithmic series of concentrations immediately after infestation. Depending on the nature of the material, application was made in one of three ways: (1) as a finely divided powder mixed with the soil and diluted with untreated soil having the same inoculum concentration; (2) as a suspension (prepared by adding 1 part of an acetone solution of the chemical to 99 parts of water) mixed and diluted with soil in the same way; (3) as an aqueous solution applied at the required concentration directly to each container of soil after the seeds had been planted. The insecticides and herbicides are listed in Table I with their chemical names and dosage rates. Technical grade chemicals were used when available and dosages were calculated on a weight basis as parts per million of active ingredient in soil. The ranges of concentrations selected for tests included the highest rate recommended for field application and extended both above and below this level. In computing dosage rates, 1 lb. per acre was taken as equivalent to 1 p.p.m. by weight of soil.

Plant bands (2″ × 2″ × 3″) were filled, in triplicate, with the various treated and infested soil mixtures and planted at a uniform depth with ten barley seeds of the variety O.A.C. 21. Soil moisture was maintained as nearly as possible at the optimum for plant growth by daily watering. The average height of seedlings in each band a week to ten days after planting was taken as a measure of the effect of the chemical being tested on both host development and disease development. The seedlings were then removed from the soil and their roots washed so that the degree of rootrot infection could be observed.

RESULTS

It was found that the insecticides and herbicides tested could be separated into four groups on the basis of their effect on the growth of barley seedlings in non-infested soil and their effect on the development of rootrot in seedlings grown in infested soil. Most of the chemicals caused stunting and other phytotoxic effects when applied at the higher dosage rates, but within the range of concentrations tolerated by barley seedlings differences appeared, some chemicals causing stimulation of plant growth and others having no effect. The chemical effects on disease development varied from decreased infection to increased infection in comparison with the controls.

The chemicals tested are grouped in Table I according to their effect on the growth of barley seedlings and on disease development:

Group A. Chemicals placed in this group had no apparent effect on either the growth of barley seedlings or on disease development. Thus, all seedlings grown in soil with the same inoculum content were essentially of equal height and showed the same degree of infection, regardless of the

TABLE 1.—INSECTICIDES AND HERBICIDES EXAMINED FOR THEIR EFFECT ON THE DISEASE OF BARLEY SEEDLINGS CAUSED BY *Helminthosporium sativum*

Group[1]	Common name	Chemical name	Dosage range (p.p.m.)
A	schradan[2]	bis (dimethylamino) phosphonus anhydride	50–800
	isodrin[2]	1,2,3,4,10,10-hexachloro-1,4,4a,5,8,8a-hexahydro-1:4, 5:8-*endo-endo*-dimethano-naphthalene	25–40
	DCU[3]	bis(1-hydroxy-2:2:2-trichloroethyl)urea	0.62–10
	IPX (sodium salt)	sodium isopropyl xanthic acid	0.62–10
	IPC[3]	isopropyl N-phenylcarbamate	0.25–4
	TCA (sodium salt)[3]	trichloroacetic acid	0.06–10
B	lindane[2]	gamma-1:2:3:4:5:6 hexachloro*cyclo*hexane	25–400
	dieldrin[2]	1,2,3,4,10,10-hexachloro-6,7-epoxy-1,4,4a,5,6,7,8,8a octohydro-1,4,5,8 dimethano-naphthalene	5–80
	DDT[2]	1:1:1-trichloro-2:2-di(*p*-chlorophenyl)ethane	6.2–100
C	maleic hydrazide[3]	1:2-dihydropyridazine-3:6-dione	0.06–1
	heptachlor[2]	1,4,5,6,7,8,8a-heptachloro-3a,4,7,7a-tetrahydro-4,7-*endo*-methanoindene	5–80
D	aldrin[2]	1,2,3,4,10,10-hexachloro-1,4,4a,5,8,8a-hexahydro-1:4,5:8-dimethano-naphthalene	2.5–80
	endrin[2]	1,2,3,4,10,10-hexachloro-6,7-epoxy-1,4,4a,5,6,7,8,8a-octahydro-1,4,5,8-*endo-endo*-dimethano-naphthalene	5–80
	chlordane[2]	2,3,4,5,6,7,8,8-octochlor-3a,4,7,7a-tetrahydro-4:7-methanoindan	2.5–40
	NPA[3]	N-1-naphthyl phthalamic acid	0.6–10
	2,4-D(amine)[3]	2,4-dichlorophenoxyacetic acid	2.5–40
	monuron[3]	3-(*p*-chlorophenyl)-1:1-dimethyl urea	0.3–5.0
	DNBP (alkanol-amine salts)[3]	4-6-dinitro-ortho-*sec.*-butylphenol	0.6–10
	dalapon (sodium salt)[3]	2-2-dichloro-propionic acid	0.6–10

[1] Grouping based on the effect of chemical on host plant and disease development (see text).
[2] Insecticide.
[3] Herbicide.

dosage of chemical applied, up to the concentration causing stunting. The plant height data for schradan, a typical Group A chemical, are presented as a three-dimensional graph in Figure 1A so that the effect of both variable factors, soil inoculum content and chemical dosage, may be compared directly.

An unusual effect was observed when the soil was treated with TCA. In non-infested soil, 0.06 to 1.0 p.p.m. TCA had no effect on the host; 1.25 p.p.m. caused slight stunting; while higher concentrations produced aborted, short-lived, blue-green seedlings. In infested soils, on the other hand, 2.5 p.p.m. TCA had no effect where 5 to 15 per cent inoculum was present, and 5 p.p.m. had no effect at the higher inoculum levels. Thus the inoculum in some way counteracted the phytotoxicity of this chemical.

Group B. Chemicals in this group stimulated the growth of barley seedlings without altering the degree of rootrot infection. The effect of lindane on plant heights is represented in Figure 1B. In non-infested soil and

at each inoculum level the heights increased as the chemical dosage increased up to 20 p.p.m. and then decreased; yet all plants from soil infested to the same degree showed equal rootrot infection. Thus treating soil with Group B chemicals resulted in more vigorous seedlings, due to chemical stimulation, not disease control.

Group C. Chemicals in this group also stimulated the growth of seedlings, as indicated by the heights of seedlings grown in non-infested soil. In infested soils, however, this beneficial effect was more than offset by an increase in severity of rootrot so that shorter plants resulted from chemical treatment. The effect of maleic hydrazide may be seen in Figure 1C. With 0 and 5 per cent inoculum in the soil the plant heights increased as the chemical dosage increased; at higher inoculum levels the heights decreased as the chemical increased. Washed roots of the latter plants showed a progressive increase in severity of rootrot with increasing chemical dosage.

Group D. The chemicals listed in the final group had no stimulatory effect on barley seedlings but improved those grown in infested soils by reducing the severity of rootrot infection. The plant height data for aldrin treatments are presented in Figure 1D. Aldrin treatments up to 10 p.p.m. had virtually no effect on the height of seedlings grown in non-infested soil, while higher concentrations reduced it. In infested soils, however, the plant heights increased with increasing concentrations, even to 40 p.p.m. That this effect was correlated with a reduction of rootrot may be seen from the photograph (Figure 2) of one replicate of these plants.

Figure 3 illustrates a set of barley seedlings growing in soils treated with NPA, another chemical of Group D. Not only has the chemical improved the seedlings by reducing rootrot, but the inoculum has in some way overcome the phytoxic effects of the highest concentration of the chemical (stunting, rolling and distortion of leaves).

EFFECT OF INSECTICIDES AND HERBICIDES ON *H. SAVITUM* IN CULTURE

In order to determine to what extent the effect of an insecticide or herbicide on disease development could be attributed to a direct effect on the causal organism, each of the chemicals was tested for toxicity to *H. sativum* in culture. For this purpose tubes of Czapek's agar were made up with a series of concentrations of each chemical in solution or suspension, the required amount of chemical being added to each tube as either a water or acetone solution after autoclaving. The final acetone content of the medium, where present, was 2 per cent. Insecticides were tested at 12.5, 25, 50 and 100 p.p.m., and herbicides at 1.24, 2.5, 5 and 10 p.p.m., to cover the dosage ranges tested in the disease trials. The tubes were cooled to 50°F., inoculated with spore suspension, shaken, and sloped for final cooling and solidification. After incubation at room temperature the relative amounts of mycelial growth were observed. DNBP was the only chemical to affect the growth of *H. sativum*, retarding it at 1.25 p.p.m. and inhibiting it completely at higher concentrations.

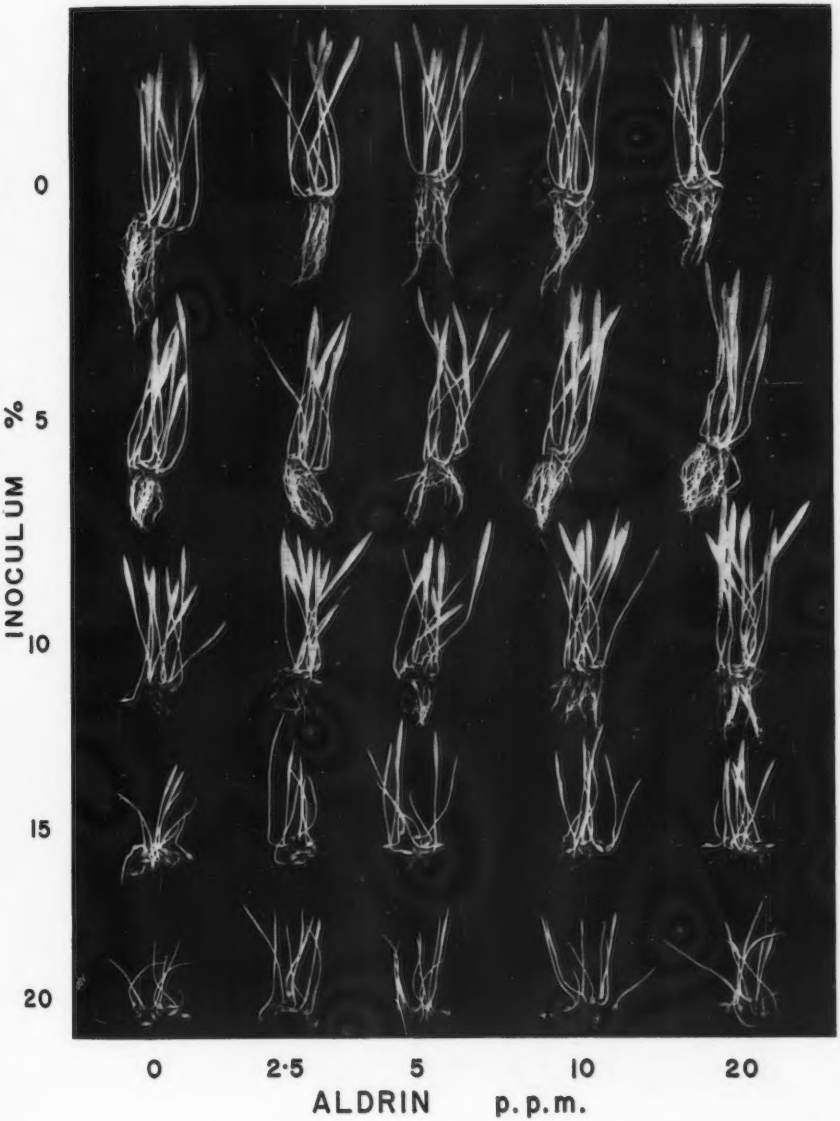


FIGURE 2. The effect of aldrin applied to soils infested with *Helminthosporium sativum* on rootrot and height of barley seedlings.

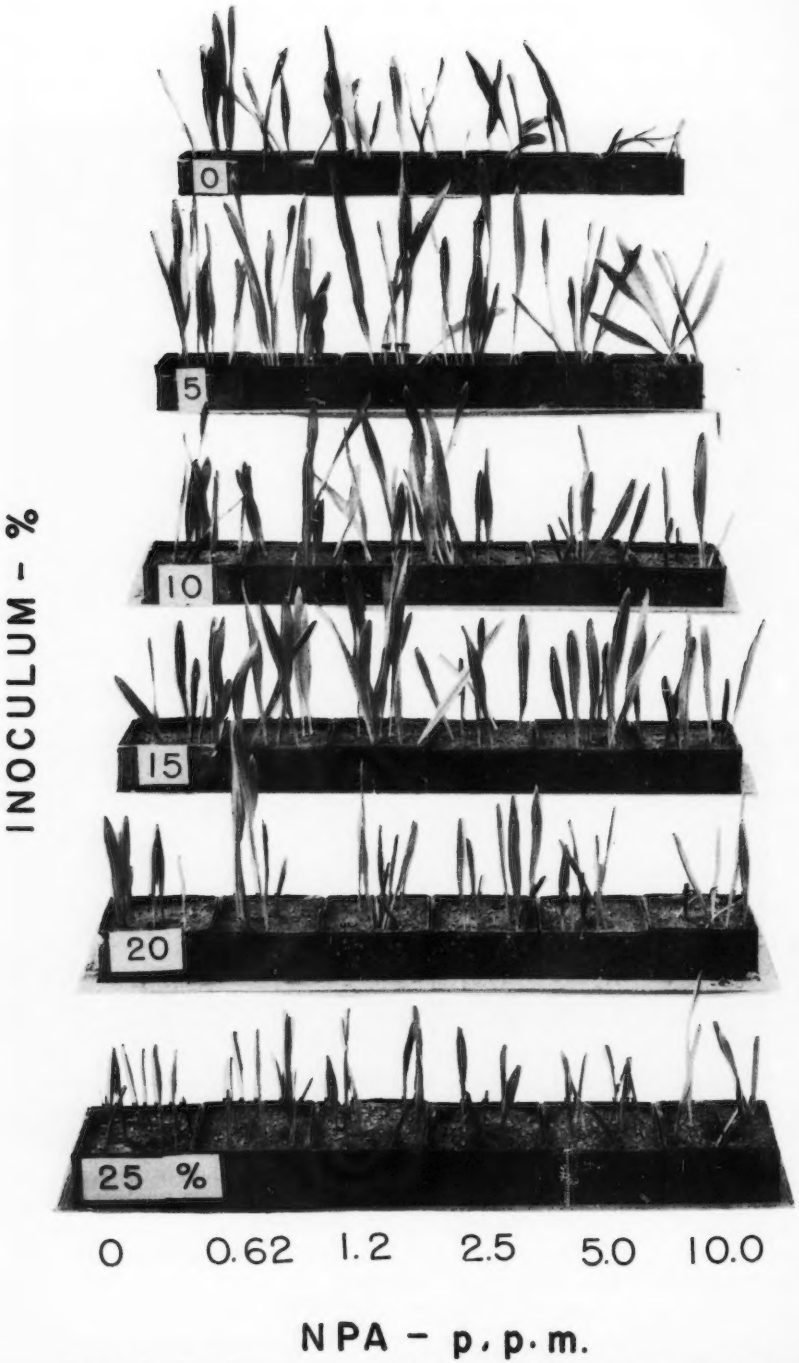


FIGURE 3. The effect of naphthyl phthalamic acid applied to soils infested with *Helminthosporium sativum* on the height of barley seedlings.

Since the hydrogen-ion concentration of the medium is known to affect the toxicity of many compounds (21), the experiment was repeated using a buffered synthetic medium adjusted to pH levels 2.5, 5.5 and 7.5. Again only DNBP was fungitoxic and its effect did vary with the acidity of the medium. At pH 3.5 growth was inhibited by 1.25 p.p.m. DNBP; at pH 5.5 growth was retarded by 2.5 p.p.m. and inhibited by 5.0 p.p.m., at pH 7.5 growth was only retarded by 10.0 p.p.m.

DISCUSSION

From the results of these studies it appears unlikely that the application of these insecticides and herbicides to the soil will aggravate the disease of barley seedlings caused by *Helminthosporium sativum*. Only two of the nineteen chemicals tested gave any indication of increasing the degree of infection, whereas eight were beneficial in that they reduced infection and the remainder had no effect on disease development.

The mechanism of action of these chemicals which did affect disease development is a matter of speculation. Since only one chemical, DNBP, was toxic to *H. sativum* in culture, the effect cannot be explained in all cases by a direct action of the chemicals on the causal organism. It is possible that the chemicals alter the metabolism of the host in a way which increases or decreases its resistance to the disease. There was no apparent relationship between effect on disease development and chemical structure. Aldrin and dieldrin, for example, were not grouped with their isomers isodrin and endrin.

ACKNOWLEDGEMENTS

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THE INFLUENCE OF COMBINED NITROGEN ON NODULATION AND NITROGEN FIXATION BY *RHIZOBIUM MELILOTI* DANGEARD[1]

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ABSTRACT

Studies to determine the effect of various concentrations of sodium nitrate and ammonium chloride on the ability of *Rhizobium meliloti* to infect and fix nitrogen in three varieties of alfalfa indicated that nodulation was inhibited at high levels of combined nitrogen. High nitrate concentrations inhibited nodulation to a greater extent than high ammonium concentrations. A small amount of combined nitrogen, however, appeared to promote nodulation. Inoculated plants grown in nitrogen levels which might be encountered in the field consistently contained more nitrogen than uninoculated plants under the same treatment. There was comparatively little difference in the nitrogen content or behaviour of the varieties of alfalfa tested.

INTRODUCTION

It is generally considered that combined forms of nitrogen depress both the nodulation of legumes and the fixation of atmospheric nitrogen. The literature on the subject is extensive and has been adequately covered elsewhere (4). With the development of the concept of a carbohydrate: nitrogen relation, principally through the efforts of Wilson (12), it is realized that the depressing effect of combined nitrogen will vary, depending upon the concentrations used and upon the rate of carbohydrate synthesis occurring in the plant. The failure to recognize the relationship between the carbohydrate and nitrogen supplies of the plant could conceivably account for the wide discrepancies that exist in the literature concerning the action of nitrogenous compounds on symbiotic nitrogen fixation and its attendant processes. In fact, the theory that it is inadvisable to inoculate legume seed which is to be planted in a high nitrogen soil may be entirely erroneous under climatic conditions fostering a high rate of photosynthesis. It also is possible that the variety of host plant might exert a modifying influence on the activity of combined nitrogen, and it was to study this particular effect that the present study was initiated.

METHODS

The host plants, consisting of Ontario Variegated, Grimm and Ranger varieties of alfalfa, were grown under greenhouse conditions, employing the sterile growth assemblies of Leonard (7). The methods of seed sterilization, inoculation with *Rhizobium meliloti*, strain R_{21}, seeding and general care of the young plants have previously been described (6). The nutrient solution employed was that used by Davis and Hoagland (3), except that the nitrogen source was omitted. Solutions of reagent grade ammonium

[1] Contribution from Department of Bacteriology, Ontario Agricultural College, Guelph, Ont., based on part of thesis submitted by senior author to the Faculty of Graduate Studies, University of Toronto, in partial fulfilment of the requirements for the Degree of Master of Science in Agriculture. (Part of the program of the Legume Research Committee in Ontario).

[2] Assistant Professor.

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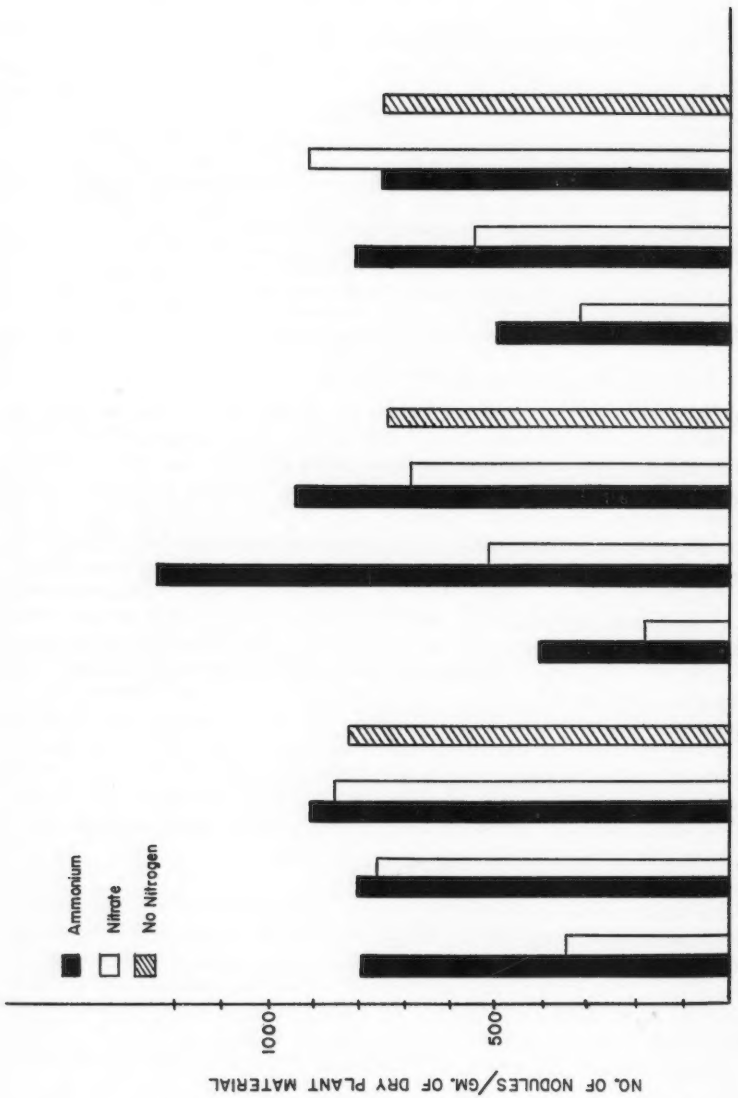

FIGURE 1. The effect of combined nitrogen on the ability of *Rhizobium meliloti* strain R_{21} to infect three varieties of alfalfa.

chloride and sodium nitrate were sterilized by Seitz filtration and added to the nutrient solution to yield final concentrations of 250, 50 and 2 p.p.m. of nitrate, and 72.5, 14.4 and 0.59 p.p.m. of ammonium. The ammonium levels were chosen so that the amounts of nitrogen present would correspond to those present in the various nitrate levels. In relation to field conditions the high concentration of nitrogenous compound would be representative of a soil containing an unusually high nitrogen level, while the medium concentration would represent a good soil in regard to the nitrogen level. The low concentration is equivalent to that in a poor soil. The nutrient solutions were tested at the time of preparation and at regular intervals during the growing period to determine the concentrations of nitrate and ammonium present. The analytical procedures were those described by Peech (9) and Cunningham (2). Corrections in concentrations were made when necessary.

The experiment was set up in 4 × 4 Latin squares. Each variety of alfalfa was represented by four squares with inoculated controls, receiving no nitrogen, common to all squares. The other treatments in these four squares consisted of three levels of nitrate, inoculated or uninoculated, and three levels of ammonium, inoculated or uninoculated. To provide sufficient material for analysis, two sterile growth assemblies were placed together to serve as one unit. Uninoculated control plants, receiving no nitrogen, were scattered over the greenhouse to check for possible contamination by air-borne rhizobia.

Six weeks after seeding the plants were carefully removed from the sand in the assemblies and the root systems gently washed. The nodules on the plants from each unit were counted and removed from the roots. Compound nodules were counted as 2, 3 or 4, corresponding to the number of lobes present. All the nodules from plants grown under the same treatment were combined and their leghaemoglobin contents determined as pyridine haemochromogen (6).

After removal of the roots, the green portions of the plants in each unit were dried at 110°C. to constant weight and the nitrogen content of the dried material determined by the micro-Kjeldahl method, using a copper-selenium catalyst (1). The amount of solar radiation received by the growth area during the growing period was obtained from pyroheliometer readings, and amounted to 12,560 calories per sq. cm. An analysis of variance was made using the nitrogen content per gm. of dried plant material.

RESULTS

All the inoculated plants were a dark green colour at the end of the growing period. The uninoculated plants showed a very notable gradation in colour from a dark green, in those plants grown under high levels of nitrogen, to a light green in plants grown under low levels of nitrogen. The uninoculated control plants were free from contaminating nodules.

The leghaemoglobin determinations carried out on the combined nodules from similar treatments indicated that the nodules were effective (Table I), the level for ineffectiveness being taken as approximately 50 micrograms of pigment per gm. of nodular tissue (6).

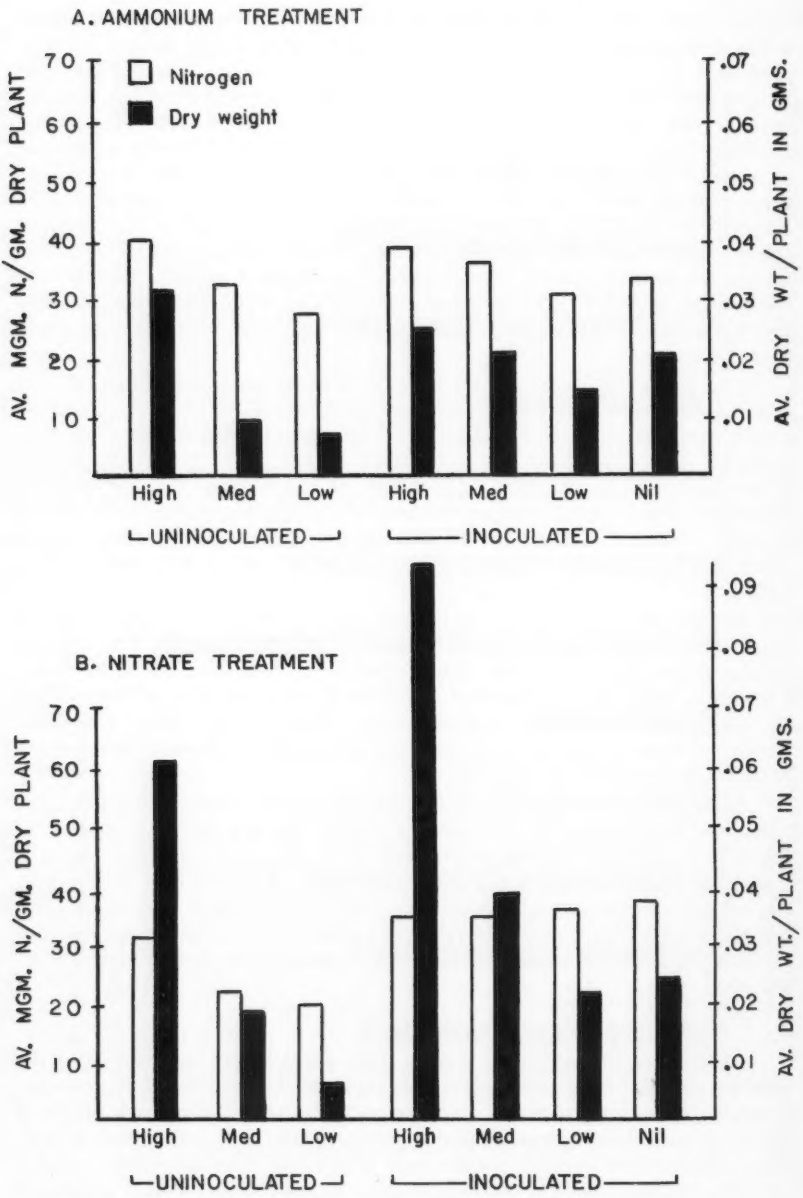

FIGURE 2. The effect of different levels of nitrogen on the nitrogen content and dry weight of Ontario Variegated Alfalfa, uninoculated and inoculated with *Rhizobium meliloti* R_{21}. Fiducial limits, based on the pooled variances within squares (with 72 degrees of freedom) for means of four observations, is equal to the mean ± 4.40.

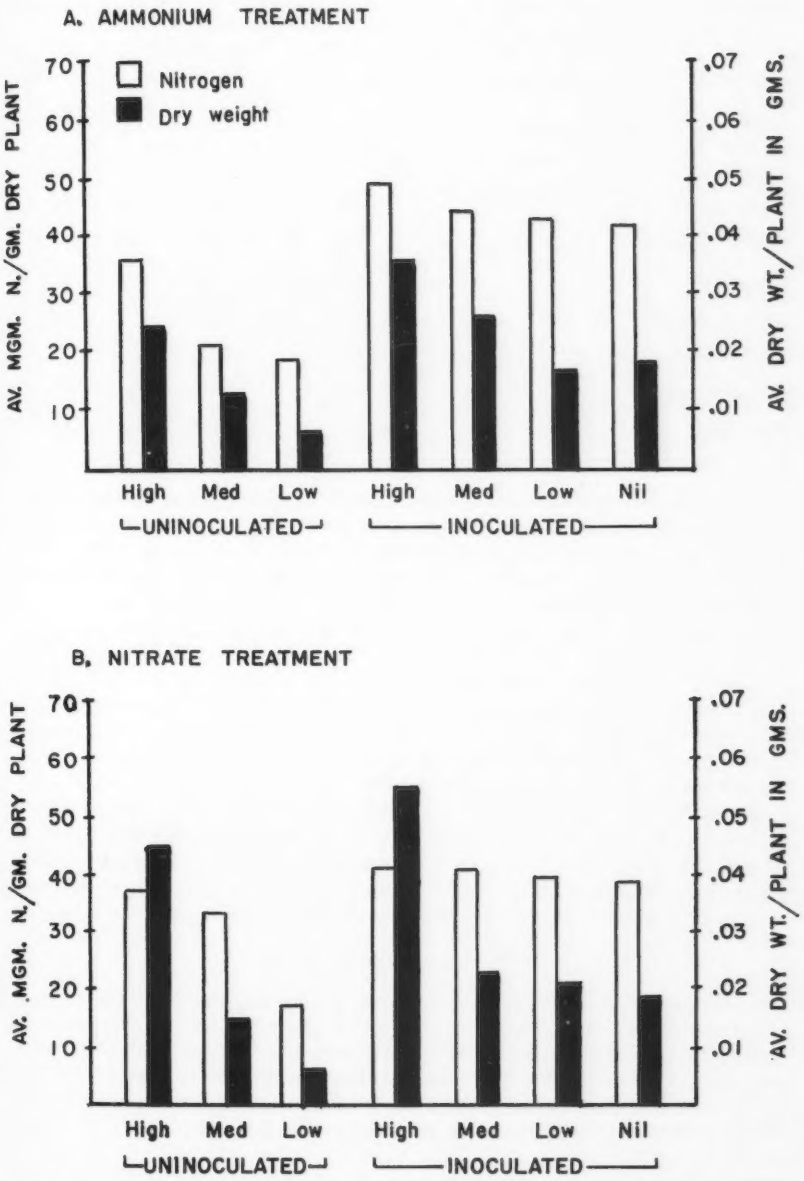

FIGURE 3. The effect of different levels of nitrogen on the nitrogen content and dry weight of Grimm Alfalfa, uninoculated and inoculated with *Rhizobium meliloti* R_{21}. Fiducial limits, based on the pooled variances within squares (with 72 degrees of freedom) for means of four observations, is equal to the mean ± 4.40.

TABLE I.—LEGHAEMOGLOBIN CONTENT IN GAMMA PER GRAM OF EXCISED NODULES FROM THREE VARIETIES OF ALFALFA INOCULATED WITH *Rhizobium meliloti* R_{21}, AND GROWN UNDER DIFFERENT LEVELS OF NITROGEN

Nitrogen treatment	Variety of Alfalfa		
	Grimm	Ont. Variegated	Ranger
High nitrate	105	135	116
Medium nitrate	129	161	203
Low nitrate	112	175	169
High ammonium	162	206	125
Medium ammonium	125	163	153
Low ammonium	114	181	193
No nitrogen	135	136	152

The extent of infection of the alfalfa varieties by *Rhizobium meliloti* strain R_{21}, is represented in Figure I. It is shown that in most cases with the highest nitrogen levels, particularly in the form of nitrate, there is an inverse relationship between the number of nodules and the amount of combined nitrogen present. With the Ontario Variegated variety, the lower levels of ammonium, but not of nitrate, promoted nodulation. With the Ranger variety, the lowest level of nitrate, but not of ammonium, promoted nodulation, while with the Grimm variety the three levels of ammonium and the two lower levels of nitrate had no significant effects on nodulation. Data pertaining to the dry weights and nitrogen contents of the plants are given in Figures 2, 3 and 4. The dry weights of the plants varied directly with increasing concentrations of substrate nitrogen, being uniformly higher with inoculated plants than with uninoculated plants. In nearly every instance more, or as much nitrogen was found in inoculated plants grown in a N-free medium than in uninoculated plants grown on any of the three levels of nitrogenous salt. The average total nitrogen contents of the host varieties are shown graphically in Figure 5.

DISCUSSION

The general results pertaining to nodulation support the observations of other workers (4, 11) who found that the infection rate decreases with increasing concentrations of combined nitrogen. It is possible that with increasing nitrogen concentrations the plant carbohydrate may be tied up in the protein-forming process to such an extent that there is little if any carbohydrate excreted from the roots into the rhizosphere. If so, there would be little inducement for the rhizobia to be attracted to the plant roots. Nevertheless, a small amount of combined nitrogen appears to be essential for optimum nodulation, as was noted by Ohkawara for other legumes (8). This may cause more rapid root growth which would produce more sites for nodule production (13), and/or enhance protein synthesis

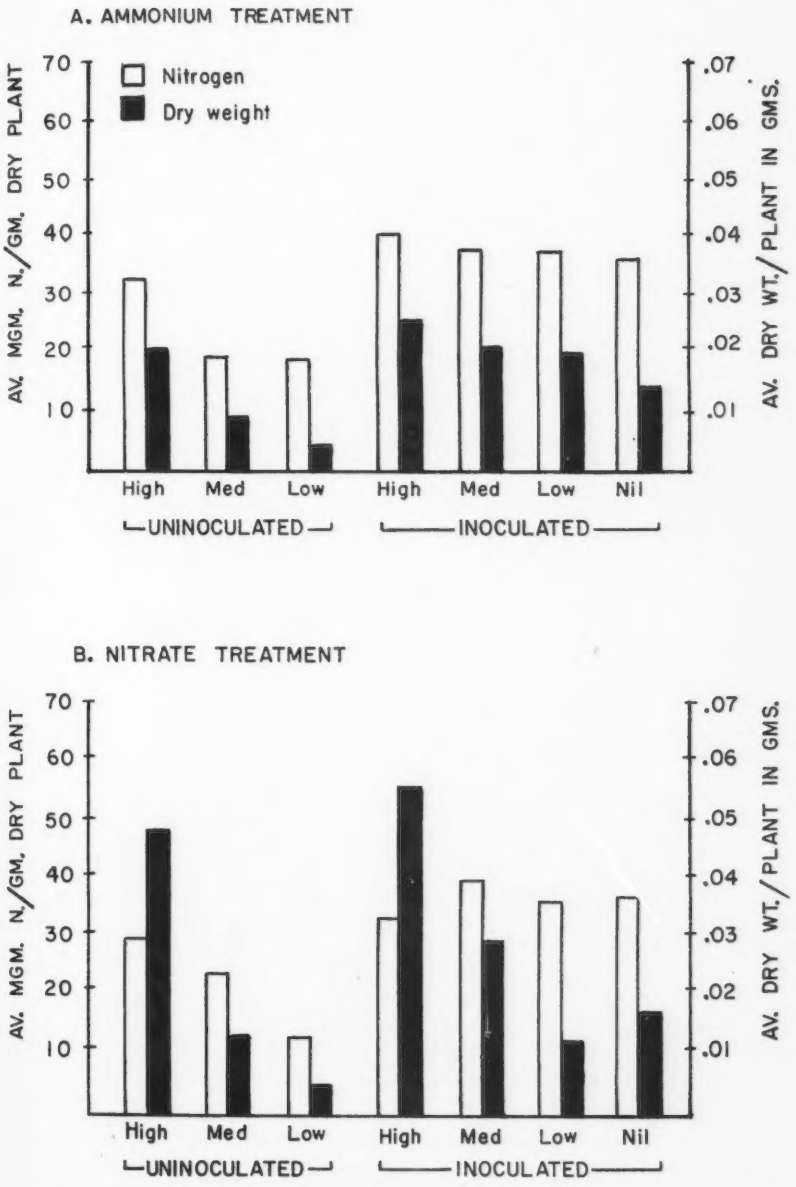

FIGURE 4. The effect of different levels of nitrogen on the nitrogen content and dry weight of Ranger Alfalfa, uninoculated and inoculated with *Rhizobium meliloti* R_{21}. Fiducial limits, based on the pooled variances within squares (with 72 degrees of freedom) for means of four observations, is equal to the mean ± 4.40.

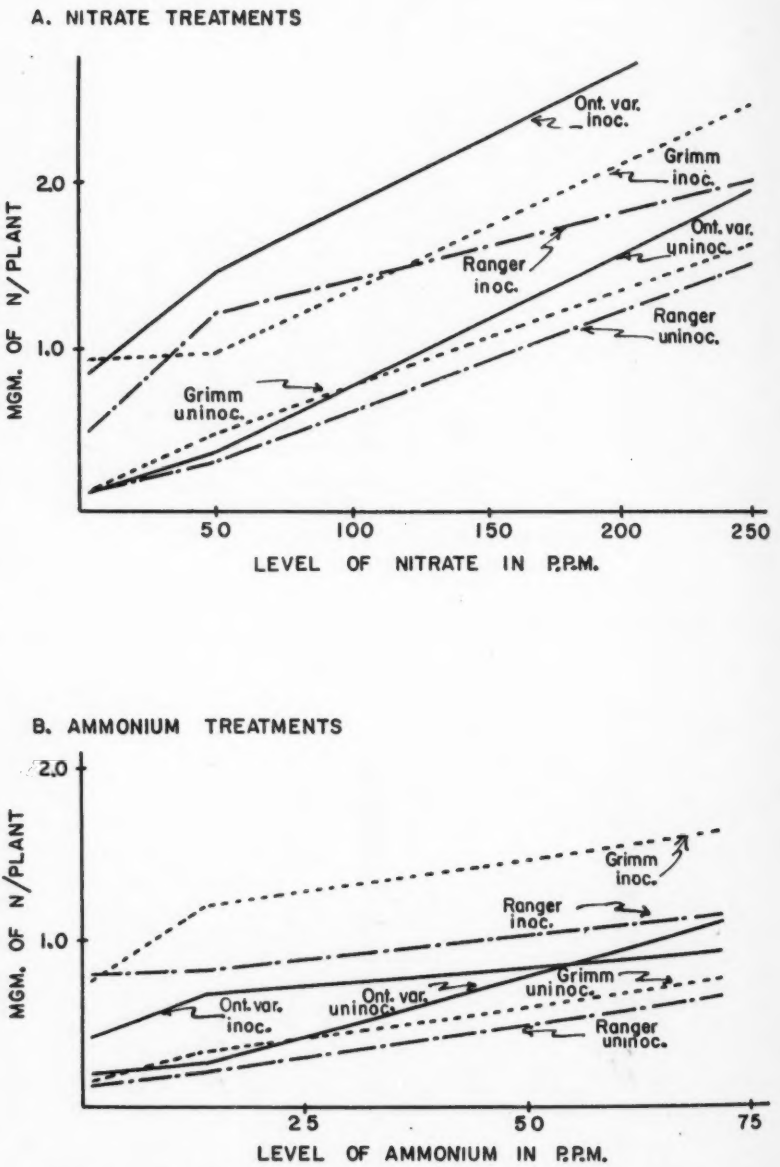

FIGURE 5. The *total* nitrogen content of three varieties of alfalfa, uninoculated and inoculated with *Rhizobium meliloti*, R_{21}, grown in different levels of nitrate and ammonium.

for the actual formation of the nodules themselves. The observation that ammonia did not decrease nodulation as much as nitrate may be a reflection of the differential effects of these compounds on the growth of the nodule bacteria (5). Strain differences in the extent of nodulation of the three host varieties are apparent from the data, but the number of nodules on a plant is not necessarily an indication of the amount of nitrogen being fixed and may not be too significant from the point of view of plant growth.

From the present study it appears that artificial inoculation of legume seed serves a useful purpose in soils low or high in nitrogen, but more benefit is derived from the inoculation of seeds which are to be planted in a field low in nitrogen. Under the solar radiation that prevailed during the growth period there was a decided tendency for inoculated plants to reach a maximum nitrogen level, regardless of whether the nitrogen was obtained from the growth substrate or the atmosphere. If this can be applied to field conditions it would seem to be unnecessary to add nitrogenous fertilizers to soils in which inoculated legumes are to be grown, unless it is added in small quantities to foster the growth of the young seedlings (12).

Varietal differences in the nitrogen contents of plants grown under comparable conditions were small and indicated that the alfalfa varieties behaved in a similar fashion to the various carbohydrate: nitrogen ratios used experimentally. However, in the present study, only the nitrogen concentration was varied. Further work in this laboratory (10) has shown that drastic changes in plant vigour are brought about by large increases in light intensity. Under conditions where the radiation received was approximately double that received by the plants in the present work (that is, 24,270 calories per sq. cm.), the inoculated plants showed only small increases in nitrogen when compared with uninoculated plants and nitrogen fixation was severely curtailed, the leghaemoglobin level in the nodules dropping to an excessively low value. A similar response has been described by Wilson (12) as occurring under a high carbohydrate: low nitrogen relationship.

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EMERGENCE OF INTERMEDIATE WHEATGRASS LINES FROM FIVE DEPTHS OF SEEDING[1]

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ABSTRACT

A study was conducted on 24 lines of *Agropyron intermedium* (Host.) Beauv. relating the size of seed to the depth from which emergence would occur. No consistent relationship was found to exist, although highly significant differences in emergence from depths of 2 inches and over did exist between lines. The results suggest that it might be worthwhile to use emergence ability from deep seedings as a selection criterion, but size of seed in itself appears to have no value.

INTRODUCTION AND LITERATURE REVIEW

The seeding of small grass seeds at too great a depth is considered to be one of the major causes for failure to obtain satisfactory stands of grasses in the arid prairie regions of Canada and the United States. However, under the prevailing climatic conditions, it is often necessary to seed 1½ inches or deeper in order to get the seed into moisture so it will germinate promptly. It would, therefore, seem desirable to select for lines or strains of grass which will emerge from a considerable depth.

Other workers (1, 2, 3) point out the desirability of having species and varieties of grass which will emerge from deep seedings and give a comprehensive review of the literature on this subject.

Rogler (3) points out the possibility of using seed weights as a criterion for selection of types of crested wheatgrass which will emerge from greater depths. He found a highly significant positive correlation coefficient for the relationship between seed weight and emergence from depths of 2 inches or greater.

The present study was conducted to determine if heavy seeded types of intermediate wheatgrass, *Agropyron intermedium* (Host.) Beauv., would emerge from a greater depth than light seeded types, with a view to using such information as a criterion for selection in a breeding program.

MATERIALS AND METHODS

The open pollinated seed from 24 clonal lines of intermediate wheatgrass was used as a seed source for this experiment. The 100-kernel weights were taken by weighing four lots of 100 hulled seeds from each line. Lines were selected to represent a seed weight range from .49 to .79 grams.

Mechanical analyses of the soil used in the study showed the following constituents: *sand*, 61.2 per cent; *silt*, 28.4 per cent; *clay*, 3.8 per cent; and *fine clay*, 6.6 per cent.

[1] Contribution from the Forage Crops Division, Experimental Farms Service.

The lines were sown in flats, measuring 15 by 17 inches and 4 inches deep. The test was designed as a four-replicate, split plot experiment with depths of 1 inch, 1½ inches, 2 inches, 2½ inches and 3 inches as the main plots and the clonal lines as sub-plots. Each flat contained six rows and they were all sown at the same depth in a particular flat. One hundred seeds were sown in each plot.

The proper depths of seeding were obtained by using wooden levellers of the required depths. The soil was levelled to the required depth in the respective flats and the seed placed in rows at that level. The flats were then filled and levelled with a quarter-inch leveller and watered.

Notes were recorded daily on the number of plants emerged from the various depths. Thirty-one days after seeding, all lines ceased to show any increase in total emergence, so the test was terminated and final counts made on all plots.

EXPERIMENTAL RESULTS AND DISCUSSION

The data and least significant differences for kernel weights, and emergence at different depths, are presented in Table 1.

Kernel Weights

Statistical analysis of the 100 kernel-weights showed that there were significant differences between clonal lines for this agronomic character.

For discussion purposes, the lines were grouped on the basis of kernel weight into three classes, namely, *light*, *medium* and *heavy* (Table 1).

Rate of Emergence

The rate of emergence of the lines, grouped into weight classes, is presented in Figure 1. As expected, an increase in the depth of seeding correspondingly delayed emergence. There was no evidence to indicate that larger seeds emerged sooner from greater depths.

Total Emergence

The experiment was designed so that individual analyses of the data for each depth could be made, as well as a complete analysis of the experiment as a whole.

The F values (Table 1) show that there were significant differences between lines for 100-kernel weights and emergence at all depths. There was also a significant interaction between depths and lines indicating that lines emerge differently from different depths.

The correlation coefficient between the 100-kernel weights and total emergence at the 3-inch depth was .148, indicating no significant relationship between seed size and the ability of various lines to emerge from deep seedings.

Satisfactory emergence was obtained with most lines in the seeding range from 1 to 2 inches deep. However, some lines such as 25377 and 25374 gave an increase in emergence with an increase in depths of seeding from 1 to 2 inches. These lines were situated in the outside row of flats, more

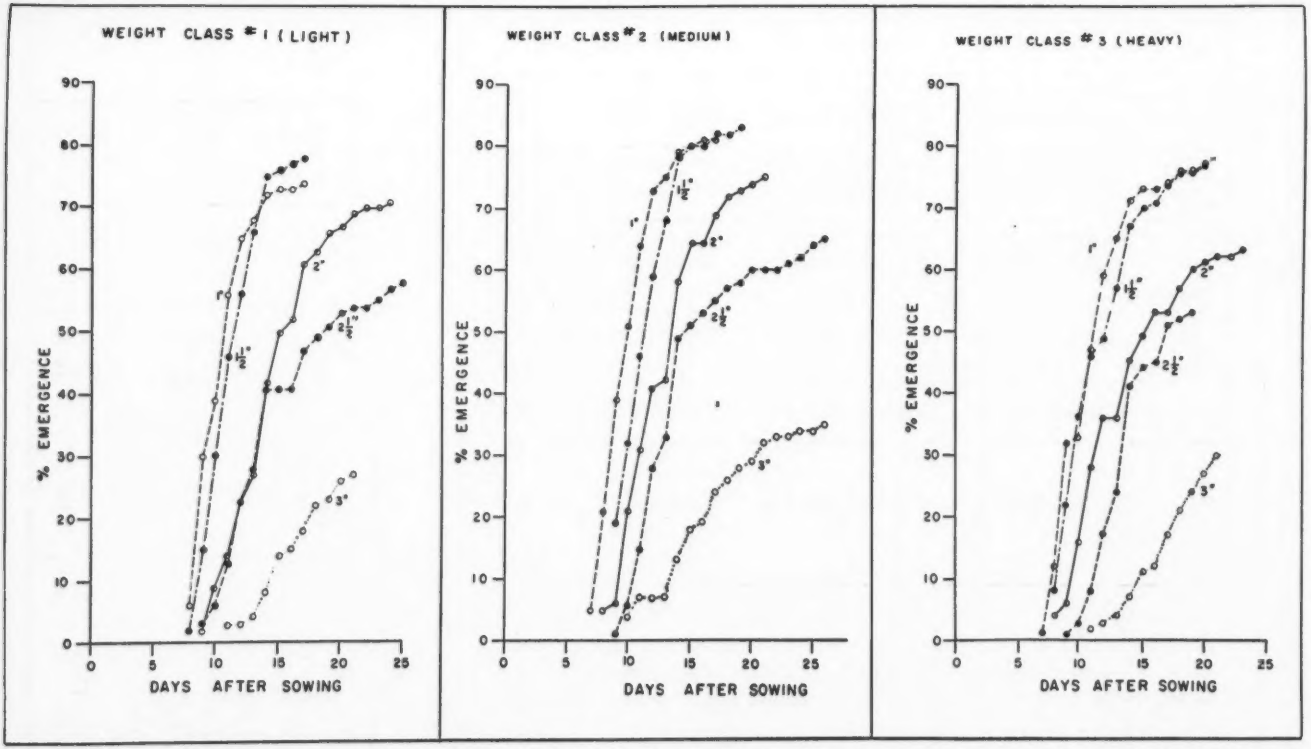

FIGURE 1. Rate of emergence of intermediate wheatgrass lines, classified into weight classes, when sown at different depths (1, 1½, 2, 2½ and 3 inches).

TABLE 1.—SUMMARY OF INTERMEDIATE WHEATGRASS DEPTH OF SEEDING EXPERIMENT

Line	100-kernel weights, grams	Average emergence from different depths—$Sin^2\theta$					
		1″	1½″	2″	2½″	3″	Mean
Weight class No. 1							
25378	.49	70.2	68.0	62.8	53.9	26.0	56.2
76	.52	61.8	63.6	54.6	48.4	28.2	51.3
69	.53	65.8	64.0	59.1	54.3	29.1	54.5
75	.53	58.9	67.2	58.6	44.8	28.3	51.6
61	.55	61.8	62.5	57.2	50.6	30.7	52.6
77	.55	47.9	55.8	60.1	50.0	35.7	49.9
74	.56	51.7	58.8	53.8	44.4	32.4	48.2
65	.58	63.1	64.3	54.8	54.1	36.2	54.5
Weight class No. 2							
25360	.61	64.5	69.2	57.2	50.4	38.4	55.9
54	.62	58.9	68.8	62.6	59.4	46.2	59.2
62	.63	67.2	67.6	61.2	63.3	45.7	61.0
63	.64	68.7	68.2	60.6	52.8	44.2	58.9
55	.66	74.6	70.8	68.4	57.6	30.3	60.3
56	.66	60.7	60.7	57.1	53.6	30.0	52.4
72	.68	66.9	68.7	62.5	53.8	28.9	56.2
50	.69	61.5	61.4	57.5	48.4	29.6	51.7
81	.69	64.8	60.2	59.2	49.6	23.8	51.5
Weight class No. 3							
25366	.70	59.2	60.2	54.8	40.6	16.1	46.2
53	.71	55.6	56.6	38.9	37.7	35.3	44.8
71	.71	62.5	70.3	55.6	48.0	33.4	54.0
57	.72	73.1	70.6	61.8	54.0	37.7	59.4
49	.73	65.3	70.0	62.2	58.6	41.5	59.5
51	.74	63.3	63.9	53.9	46.0	32.3	51.9
52	.79	57.4	44.8	43.8	42.8	31.7	44.1
Mean	.64	62.7	64.0	57.4	50.7	33.0	53.6
L.S.D. (P = .05)	.03	8.9	10.2	8.3	10.2	9.9	4.2

L.S.D. (P = .05) for depths = 5.8.
L.S.D. (P = .05) for depths × lines interaction = 5.3.
Correlation coefficient between 100-kernel weights and total emergence at 3-inch depth = .148 (not significant).

Variance Table for Split Plot Analysis

Source	Degrees of freedom	Mean square	F	F 5%	F 1%
Whole plots					
Total	19				
Replicates	3	1611.08	4.68	3.49	5.95
Depths	4	15341.20	44.60	3.26	5.41
Error 1	12	343.99			
Split-plots					
Total	479				
Lines	23	466.79	10.37	1.57	1.88
Depth × Lines	92	83.17	1.85	1.32	1.48
Error 2	345	45.02			

frequently than others, and their peculiar behaviour probably is due to differential moisture conditions. At the 2½-inch depth, several lines showed a marked reduction in total number of plants emerged, and at the 3-inch depth, emergence of most lines was quite low, but four lines—25349, 25354, 25362, and 25363—still emerged to the extent of over 40 per cent. These results, and the fact that a highly significant depths × lines interaction was obtained, strongly suggest that it might be important to use emergence from a 2½ to 3-inch depth of seeding, as one selection criterion in the breeding of intermediate wheatgrass for use in a dry climate.

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SOME ASPECTS OF THE RELATION BETWEEN NECTAR SECRETION AND NITROGEN, PHOSPHORUS, AND POTASSIUM NUTRITION[1]

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ABSTRACT

The influence of mineral nutrition on nectar secretion both *per se* and in relation to certain aspects of growth and development was studied in snapdragon and red clover plants growing in sand culture. Snapdragon was grown at two levels each of nitrogen, phosphorus, and potassium, red clover at three levels each of phosphorus and potassium. The volume of nectar and weight of nectar sugar secreted per inflorescence were affected by the supply of each of the elements studied. Secretion in snapdragon was favoured by the lower levels of nitrogen, phosphorus, and potassium. Secretion in red clover was best at the low and intermediate levels of phosphorus and at the intermediate level of potassium. Although a high concentration of phosphorus or potassium in the mineral supply reduced secretion in both species, the threshold concentration for this inhibitory effect was higher in red clover than in snapdragon. High concentrations of potassium consistently reduced the sugar concentration of the nectar in both species. Flower number as well as quantity of secretion per inflorescence varied with nutritional treatment. For maximal production of nectar by the plant, the following conditions of fertility would appear desirable: A level of nitrogen low enough to avoid excessive vegetative growth, a level of phosphorus sufficient to promote good flowering, and a level of potassium which is neither low enough to limit growth severely nor high enough to reduce flower production.

INTRODUCTION

The secretion of nectar by floral nectaries is of special interest to two agricultural groups—beekeepers and seed or fruit producers. To the first group, nectar is a crop. To the second, nectar secretion is a link in the chain of events leading to fruit production, for the relationship between insect-pollinated plants and their pollinators is often built around nectar. The availability, quantity, and concentration of nectar govern the attractiveness of nectar plants to bees (4, 20), and when plants are dependent on bees for pollen transfer, one or more of these features may limit bee visitation and pollination (10, 21).

Although the mechanism is not understood, nectar secretion does appear to depend on metabolic activity in the nectary (8, 16, 24). The quantity secreted is a function of the carbohydrate supply to the nectary (16, 23). The concentration at which nectar leaves the nectary cells appears to depend on the anatomy of the vascular system supplying the nectar and on the sugar concentration in the phloem and/or xylem of the nectary vascular supply (1, 16). While standing in the flower nectar usually becomes considerably more concentrated as a result of evaporation (14).

Several studies of the effects of nitrogen, phosphorus, and potassium on nectar secretion have been conducted in recent years, but the results are conflicting. Schöntag (13) could detect no improvement in nectar

[1]Contribution of the Apiculture Department, Ontario Agricultural College, Guelph, Ont. The work reported herein has been a part of the program of the Legume and Tree Fruit Research Committees in Ontario.

secretion in several species as a result of adding nitrogen, phosphorus, and potassium to the soil, although fertilizer additions increased flower production. Sistak [cited in (3)] found that citrophosphate increased nectar yield and bee visits in fields of white clover and beans (*Vicia faba*). Veprikov [cited in (3)] found that extra phosphorus and potassium enhanced nectar secretion, bee visitation, and seed yield in buckwheat. Hasler and Maurizio (9) noted that potassium-deficient soil supported poor nectar yields. Stapel and Götzache (18), on the other hand, found that potassium manuring lowered nectar production in fields of red clover.

Such lack of agreement may have been due in part to failure to relate effects of fertilizer additions on secretion to indices of sufficiency or deficiency of the elements in question, as for example the initial fertility level of the soil, concentration of mineral elements in the plant tissue, or measurements of plant growth. Ryle (12) recently conducted an excellent study of the influence of variation in the supply of nitrogen, phosphorus, and potassium on growth and nectar secretion in several plant species in sand culture. She found that when potassium was limiting to growth, nectar secretion was generally poor, whereas nectar secretion was good when potassium was present in abundance relative to nitrogen and phosphorus. Low levels of nitrogen favoured secretion in mustard. Mustard plants secreting large amounts of nectar were comparitively weak vegetatively and tended to have relatively intense red pigmentation in withered leaves. Such plants are probably high in carbohydrate relative to their nitrogen content. Shuel (15), noting abundant nectar secretion under conditions of low nitrogen supply, moderate growth, and a high plant sugar content, suggested that part of the variation in secretion with nitrogen supply might be explained on the basis of limitations imposed on growth by relative deficits of sugars or nitrogenous compounds.

The purpose of the investigations reported herein was twofold: (i) to measure nectar secretion under conditions of a controlled supply of nitrogen, phosphorus, and potassium; and (ii) to seek possible relationships between concomitant variation in secretion and plant development.

MATERIALS AND METHODS

Red clover (*Trifolium pratense* L.) and snapdragon (*Antirrhinum majus* L.) were chosen as representatives of leguminous and non-leguminous plants, respectively. Red clover is an important forage plant in which nectar secretion may be limiting to pollination under Ontario conditions. Snapdragon is of little economic importance as a nectar plant, but may be considered representative of many non-leguminous honey plants. It is an excellent subject for nectar studies. Genetic variability was minimized by using hybrid snapdragon plants of the F_1 generation and a clonal population of red clover. Experiments were done in a greenhouse equipped with automatic steam valves set for 65°F. Night temperatures remained constant within a few degrees. The high day temperatures common in greenhouses during sunny weather were reduced by careful control of vents and by whitewashing the exterior in the summer months.

Plants were grown in pure silica sand in 10-inch pots, sub-irrigated daily with a solution containing all mineral elements essential for growth.

Those elements present in high concentration were supplied as sodium nitrate, ammonium chloride, potassium sulphate, sodium dihydrogen phosphate, calcium chloride, and Epsom salts; the exact concentration of each element is listed in the next section of the narrative. Boron, zinc, manganese, copper, molybdenum, and iron (as ferric tartrate) were added at concentrations of 0.45, 0.05, 0.6, 0.02, 0.04, and 1.7 p.p.m., respectively. Solutions were made up with distilled water, and pH's were maintained at 6.0 to 6.5 with additions of normal sodium hydroxide and hydrochloric acid. Variation in osmotic pressure was kept within 0.05 atmospheres by adding appropriate amounts of sodium chloride to solutions low in total salts. Solutions were changed every nine or ten days and were made up to initial volume with distilled water between changes. No record was kept of fluctuations in the composition of solutions between changes; instead, the mineral composition of the plant tissue at the conclusion of the experiment was used as an index of mineral uptake.

Experimental Designs

The snapdragon experiment was arranged in a factorial design comprising all possible combinations of two levels each of nitrogen, phosphorus, and potassium. The concentrations of these elements were as follows:

N_1 — 30 p.p.m.; N_2 — 150 p.p.m.
P_1 — 13 p.p.m.; P_2 — 65 p.p.m.
K_1 — 36 p.p.m.; K_2 — 180 p.p.m.

Nitrogen was supplied as sodium nitrate. Calcium was supplied at 200 p.p.m. and magnesium at 48 p.p.m. in all treatments. Because of the wide variation in concentration of the elements under study, it was not possible to keep the concentration of sodium, chlorine, and sulphur the same in all treatments. Sodium concentration varied from 330 to 355 p.p.m. in low-potassium treatments and from 285 to 300 p.p.m. in high-potassium treatments. Sulphur concentration was 79 p.p.m. in low-potassium treatments and 138 p.p.m. in high-potassium treatments. Chlorine varied from 640 to 780 p.p.m. in low-nitrogen treatments and from 325 to 460 p.p.m. in high-nitrogen treatments.

Five seedlings of the hybrid "Star Charter", 4 or 5 inches in height, were assigned to each treatment in August, 1953. Plants were pruned to produce two flowering stems.

Because of limitations on space, it was decided to omit the nitrogen variable from the red clover experiment, and to test the effects of phosphorus and potassium at three levels. A factorial design was used which incorporated all combinations of the following levels of the two elements:

P_1 — 10 p.p.m.; P_2 — 40 p.p.m.; P_3 — 160 p.p.m.
K_1 — 8 p.p.m.; K_2 — 45 p.p.m.; K_3 — 180 p.p.m.

Nitrogen was supplied at 102 p.p.m. in all treatments, half as sodium nitrate and half as ammonium chloride. A high concentration of nitrogen was adopted on the assumption that inter-treatment differences in nitrogen produced in nodules would be relatively unimportant if the external source were abundant. Calcium and magnesium were supplied at 300

and 96 p.p.m., respectively. Sodium was present at 275 p.p.m. in K_1 treatments, 260 p.p.m. in K_2 treatments, and 200 p.p.m. in K_3 treatments; sulphur at 130 p.p.m. in K_1 treatments, 145 p.p.m. in K_2 treatments, and 200 p.p.m. in K_3 treatments. The concentration of chlorine varied with both potassium and phosphorus supply from 815 p.p.m. in the P_1K_1 treatment to 525 p.p.m. in the P_3K_3 treatment.

Young red clover plants developing from crown divisions made in December, 1954, were transferred to sand culture in early March, 1955, four plants to each treatment. They were exposed to the normal seasonal day length until the first of June to permit strong vegetative growth to take place. The photoperiod was then lengthened to 18 hours with supplementary incandescent illumination of about 100 f.c. intensity.

Nectar Measurements

Flowers were harvested daily as soon as they were fully expanded. Nectar assay was by the centrifugation method, in which flowers are inverted and centrifuged in special capillary tubes calibrated for volume (19). Concentrations of total solids were measured with an Abbé refractometer in terms of equivalent concentrations of pure sucrose. As nectar usually contains glucose and fructose as well as sucrose (22), and trace amounts of other solids, concentration values obtained by this method are not strictly accurate, but are satisfactory approximations.

Nectar secretion was recorded on the basis of:

(*a*) *Volume of Nectar per Flower*—The volume of nectar in the flower is an index of the availability of nectar to the pollinator.

(*b*) *Nectar Concentration*—The concentration of sugar (or more accurately, total solids) in nectar also influences the attractiveness of the flower to pollinating insects.

(*c*) *Weight of Nectar Sugar per Flower*—Volume and concentration values have one serious limitation. There is no way of distinguishing between variation in nectar concentration at the moment of secretion and post-secretion changes resulting from evaporation. The latter changes affect both volume and concentration. The use of weights of nectar sugar overcomes this difficulty, as it comprises variation in both volume and concentration. Weight of nectar sugar can be used as a measure of the intensity of secretion and of the attractiveness of the flower to insects.

(*d*) *Weight of Nectar Sugar per 100 Florets*—It is convenient to express nectar secretion in red clover on the basis of 100 florets rather than a single floret.

(*e*) *Weight of Nectar Sugar per Flower Head*—Variation in nectar yield among red clover inflorescences is due partly to differences in the intensity of secretion and partly to differences in number of florets. Both variables may be influenced by mineral nutrition.

(*f*) *Estimated Weight of Nectar Sugar per Plant*—This quantity is the product of nectar sugar per flower (or inflorescence) and number of flowers per plant.

Recording of Other Data

Weather records were kept for the period of nectar harvest. Solar radiation values were obtained from a recording potentiometer connected to a pyrheliometer. Vapour pressures were calculated from meteorological records of relative humidity at 1 p.m. daily and maximum daily temperatures (usually attained in mid-afternoon).

Records were kept of plant weights, numbers, weights of flowers, and flowering dates. When flowering had ceased, plant tops were weighed, dried in a hot air blast (15) ground in a Wiley mill, and further dried in an oven in preparation for chemical analysis. Standard methods of

analysis (2) were followed: Reducing sugars were determined by the Lane-Eynon volumetric method, sucrose from reducing sugars before and after inversion, and starch by the calcium chloride method. As it was later realized that oven-drying might lead to inaccuracies in values for individual sugars as a result of sucrose hydrolysis, values for reducing sugars and sucrose were combined as "total sugar". Nitrogen was determined by the Gunning method, phosphorus as total phosphoric acid by the volumetric method, and potassium by flame photometry. Calcium was measured by titration with potassium permanganate, magnesium and chlorine by the respective gravimetric methods, and sulphur by oxidation with magnesium nitrate.

Statistical Evaluation of Data

Data on nectar secretion, growth, and flower production were first analysed by the analysis of variance method (17). 'F' values and standard errors of means were calculated for variation due to nutritional treatment, days, and treatment-day interactions. This analysis was followed by a factorial analysis of the main effects and interactions of nitrogen, phosphorus, and potassium (5). Correlational methods were used to assess the relationship of secretion to solar radiation and atmospheric vapour pressure.

RESULTS AND DISCUSSION

Snapdragon Experiment

Effect of Nutrition on Plant Development

The data in Table 1 indicate that uptake of nitrogen, phosphorus, and potassium was considerably greater at the upper levels in the mineral solution. Inter-treatment differences in plant development were pronounced. The lower concentrations of nitrogen and potassium limited

TABLE 1.—MINERAL COMPOSITION OF SNAPDRAGON SHOOTS AT TWO LEVELS EACH OF NITROGEN, PHOSPHORUS, AND POTASSIUM

Treatment	Mineral composition (% oven-dry weight)				
	N	P	K	Cl	S
$N_1P_1K_1$	2.08	0.238	1.78	1.96	0.222
$N_1P_1K_2$	1.87	0.257	3.06	1.53	0.297
$N_1P_2K_1$	2.13	0.319	1.82	1.85	0.264
$N_1P_2K_2$	2.30	0.323	3.08	1.33	0.281
$N_2P_1K_1$	2.82	0.206	1.55	1.36	0.280
$N_2P_1K_2$	3.02	0.241	3.56	1.15	0.279
$N_2P_2K_1$	3.28	0.361	1.82	1.42	0.336
$N_2P_2K_2$	2.87	0.294	3.50	1.24	0.277
Variation between duplicate analyses	0.08	0.005	0.05	0.02	0.010

TABLE 2.—NECTAR SECRETION IN SNAPDRAGON AT TWO LEVELS EACH OF NITROGEN, PHOSPHORUS AND POTASSIUM

Treatment	Mean fresh wt. of shoots	Mean number of flowers per plant	Mean volume of nectar per flower	Mean nectar sugar concentration	Mean weight of nectar sugar per flower	Estimated weight of nectar sugar per plant
	g		μl	%	mg.	mg.
$N_1P_1K_1$	20.6	36.8	4.78	60.4	3.13	115
$N_1P_1K_2$	28.7	32.2	5.04	56.7	3.26	105
$N_1P_2K_1$	26.3	39.4	4.65	60.1	3.29	130
$N_1P_2K_2$	27.5	34.0	3.88	58.1	2.74	93
$N_2P_1K_1$	34.0	39.2	4.99	60.0	3.56	139
$N_2P_1K_2$	42.8	27.4	3.19	56.8	2.35	64
$N_2P_2K_1$	33.0	41.4	3.77	64.1	2.81	116
$N_2P_2K_2$	35.7	46.2	3.05	59.3	2.12	98
L S D 0.05		11.0	0.72	2.7	0.47	
0.01			0.95	3.6	0.62	

L S D—Least Significant Difference.

shoot growth, whereas phosphorus supply had little effect on growth (Table 2). Flowering was influenced by both phosphorus and potassium supply. Maturation of flowers was accelerated by a high concentration of phosphorus and retarded by a high concentration of potassium. Plants grown at the higher phosphorus level had longer flower spikes and more flowers (Table 2). The combination of low phosphorus with high potassium produced strongly vegetative plants with few flowers. The higher level of phosphorus in combination with the lower level of potassium had the opposite effect. Flower weight varied inversely with nitrogen and phosphorus supply, and directly with potassium supply.

Nectar assay was begun in mid-October when daily samples of five flowers could be obtained from all treatments, and was carried on for eight days.

Effect of Nutrition on Nectar Secretion

The effects of the various combinations of the three elements are shown in Table 2. Volume of nectar and weight of nectar sugar per flower were lowest in the treatment combining the upper level of the three elements ($N_2P_2K_2$). Flowers in treatment $N_2P_1K_1$ secreted about 60 per cent more nectar than those of the $N_2P_2K_2$ treatment. The higher level of potassium consistently reduced nectar sugar concentration, irrespective of the levels of nitrogen and phosphorus with which it was combined.

The effects of the individual elements on nectar secretion and flower production are shown in Figure 1. The higher concentration of each element reduced the average weight of nectar sugar per flower significantly. The adverse effect of high concentrations of nitrogen and phosphorus may have been due in part to a reduction in flower size. A significant positive regression of nectar sugar on flower size was found earlier in snapdragon (16). Potassium, unlike nitrogen and phosphorus, had opposite effects

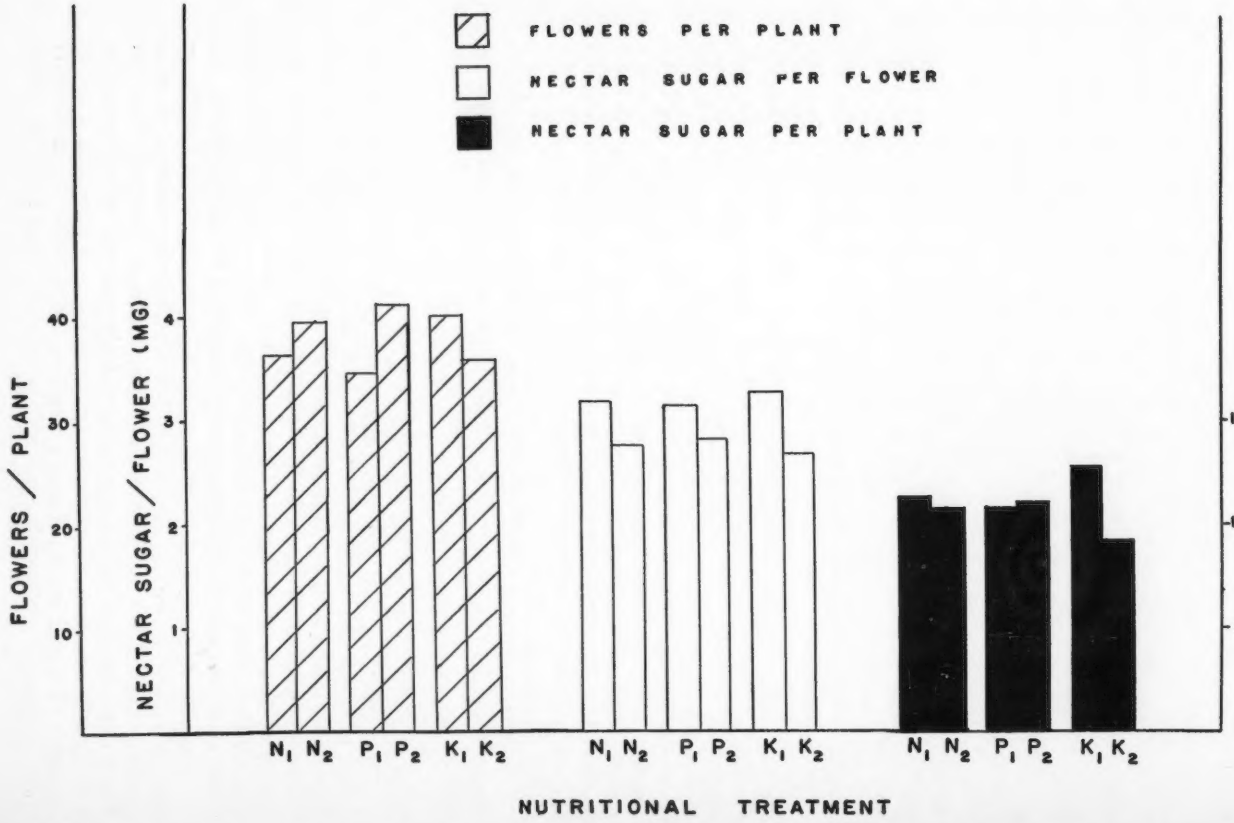

FIGURE 1. Average effects of nitrogen, phosphorus, and potassium on nectar production in snapdragon. Standard errors of mean differences: for number of flowers 2.7; for nectar sugar per flower, 0.12 mg. Standard error for nectar sugar per plant not known.

on flower weight and nectar secretion. A highly significant NK interaction was found in the factorial analysis of variance; secretion was favoured by combinations of dissimilar levels of nitrogen and potassium.

On the basis of estimated yield of nectar sugar per plant, relative differences between treatments were altered somewhat (Table 2). The nectar potential of plants in the $N_2P_1K_1$ treatment was still superior to all others, and was more than twice as great as the potential of plants in the $N_2P_1K_2$ treatment. In the latter group total nectar was reduced by low flower production as well as poor nectar secretion. Abundant flower production among plants of the $N_2P_2K_2$ treatment, which secreted less nectar per flower than other groups, raised the average nectar potential of these plants to a level comparable with that of the $N_1P_2K_2$ plants, which secreted more nectar per flower but had fewer flowers. Potassium concentration had a marked effect on total nectar yield per plant. The depressive effect on secretion of the upper levels of nitrogen and phosphorus was partially offset by their favourable influence on flower production. The higher concentration of potassium, however, reduced both nectar secretion and flower production (Figure 1).

Relationship of Nectar Secretion to Weather Factors, Growth, and Tissue Carbohydrate Content

Variation in nectar secretion from day to day was somewhat greater than variation between nutritional treatments. The range in daily yields of nectar sugar was between 1.3 and 3.9 mg. per flower. No treatment-weather interaction was found. The mean daily weight of nectar sugar per flower was positively correlated with quantity of solar radiation during

TABLE 3.—MINERAL COMPOSITION OF RED CLOVER SHOOTS AT THREE LEVELS EACH OF PHOSPHORUS AND POTASSIUM

Treatment	Mineral composition (% oven-dry weight)				
	N	P	K	Ca	Mg
P_1K_1	1.95	0.084	0.77	1.36	0.47
P_1K_2	2.14	0.108	1.92	1.37	0.45
P_1K_3	1.88	0.099	3.05	2.65	0.45
P_2K_1	2.51	0.394	0.57	2.22	0.79
P_2K_2	2.17	0.330	1.32	1.95	0.83
P_2K_3	1.77	0.314	2.68	2.07	0.63
P_3K_1	2.41	0.635	0.82	2.16	0.87
P_3K_2	2.46	0.650	3.57	1.99	0.76
P_3K_3	2.20	0.544	5.12	1.33	0.45
Variation between duplicate analyses	0.08	0.005	0.05	0.08	0.02

FIGURE 1. Average effects of nitrogen, phosphorus, and potassium on nectar production in snapdragon. Standard errors of mean differences: for number of flowers 2.7; for nectar sugar per flower, 0.12 mg. Standard error for nectar sugar per plant not known.

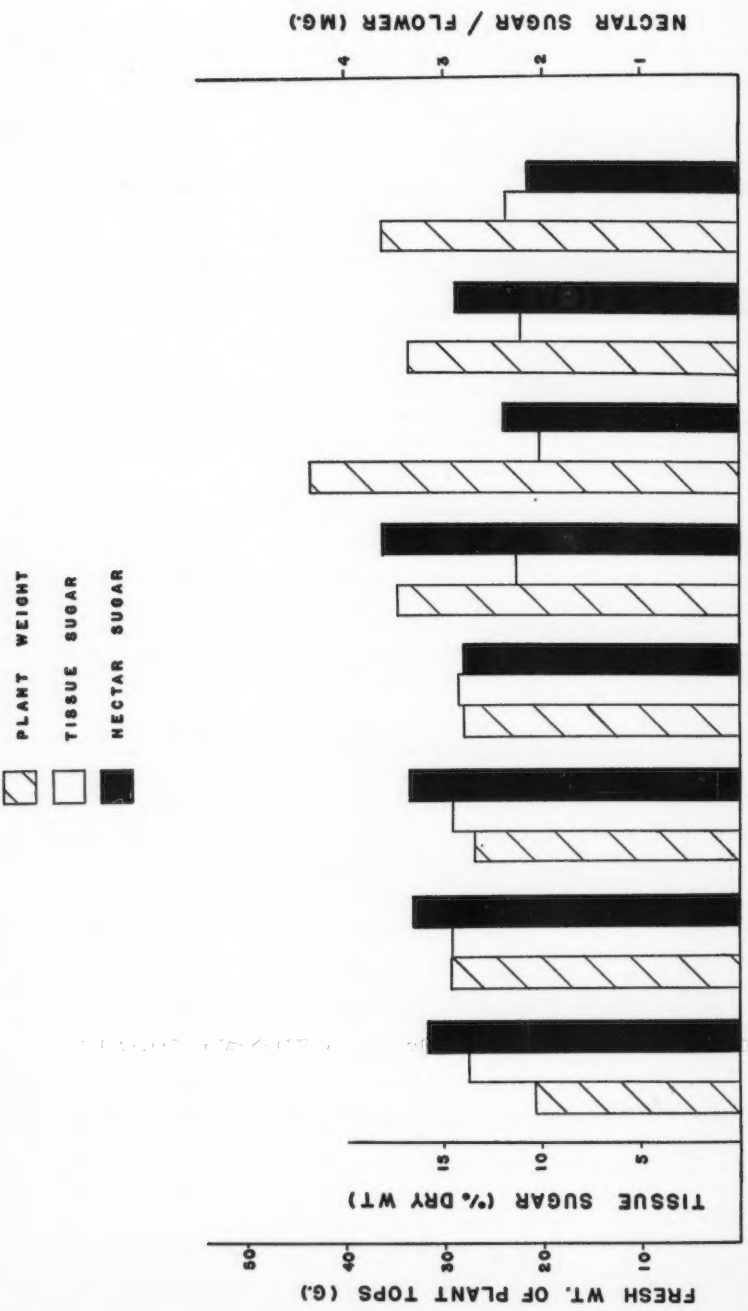

FIGURE 2. Relationship of nectar secretion to growth and tissue sugar content of snapdragon. Standard error of mean difference in nectar sugar, 0.24 mg. Difference between duplicate sugar analyses, 0.17 per cent.

the 72-hour period preceding harvest ($r = +0.735$, significant at the 2 per cent level). Nectar concentration was inversely correlated with the mean atmospheric vapour pressure for the 24-hour period preceding harvest ($r = -0.637$, significant at the 5 per cent level).

Reference has already been made to the hypothesis that the quantity of nectar secreted when nitrogen supply is varied may depend on the relative amounts of nitrogen and carbohydrate available for growth. The data in Figure 2 lend some support to this hypothesis. In general, tissue sugar content was relatively high and nectar secretion relatively good when growth was limited by a deficit of nitrogen. The $N_2P_1K_1$ treatment, in which weight of nectar sugar per flower was high in spite of a low content of tissue sugar, was an exception. Variation in phosphorus or potassium supply produced no consistent pattern of concomitant variation in growth, tissue sugar, and nectar secretion.

Nectar secretion might be described in general terms of growth and flower production thus: Secretion per flower was generally good when nitrogen and potassium supply were suboptimal for growth and when phosphorus supply was suboptimal for flower production.

Red Clover Experiment

Influence of Mineral Nutrition on Plant Development

The data in Table 3 indicate that uptake of phosphorus and potassium was proportional to their concentration in the mineral solution. It may be noted that P_3 plants were unusually high in potassium. Nitrogen content of tissue varied by about 33 per cent.

Potassium was limiting to shoot growth at the two lower concentrations (Table 4). The first increment of potassium produced a large increase in growth at the two lower levels of phosphorus and a smaller increase at the highest level. The second increment produced a relatively small increase in growth. The highest level of phosphorus reduced growth when combined with the intermediate or high level of potassium. Weight of root system was directly proportional to the potassium concentration and inversely proportional to the phosphorus concentration. As the degree of plant senescence varied between treatments in proportion to the number of flower heads produced, oven-dry weights rather than fresh weights were used as a measure of growth.

Flower production was influenced by the relative concentrations of phosphorus and potassium in the mineral solution (Table 4). Extremes were represented by plants in the treatment P_1K_3, which were strongly vegetative, and plants in the treatment P_3K_1, which were comparatively small and flowered abundantly. The largest flower heads developed at the intermediate level of potassium and the low and intermediate levels of phosphorus. The number of florets was directly related to head weight. The average length of staminal tubes varied in a complex manner with both phosphorus and potassium supply. The significance of this effect will be discussed in a later section.

An abundance of phosphorus relative to the amount of potassium in the mineral solution promoted early flowering. With the exception of

FIGURE 2. Relationship of nectar secretion to growth and tissue sugar content of snapdragon. Standard error of mean difference in nectar sugar, 0.24 mg. Difference between duplicate sugar analyses, 0.17 per cent.

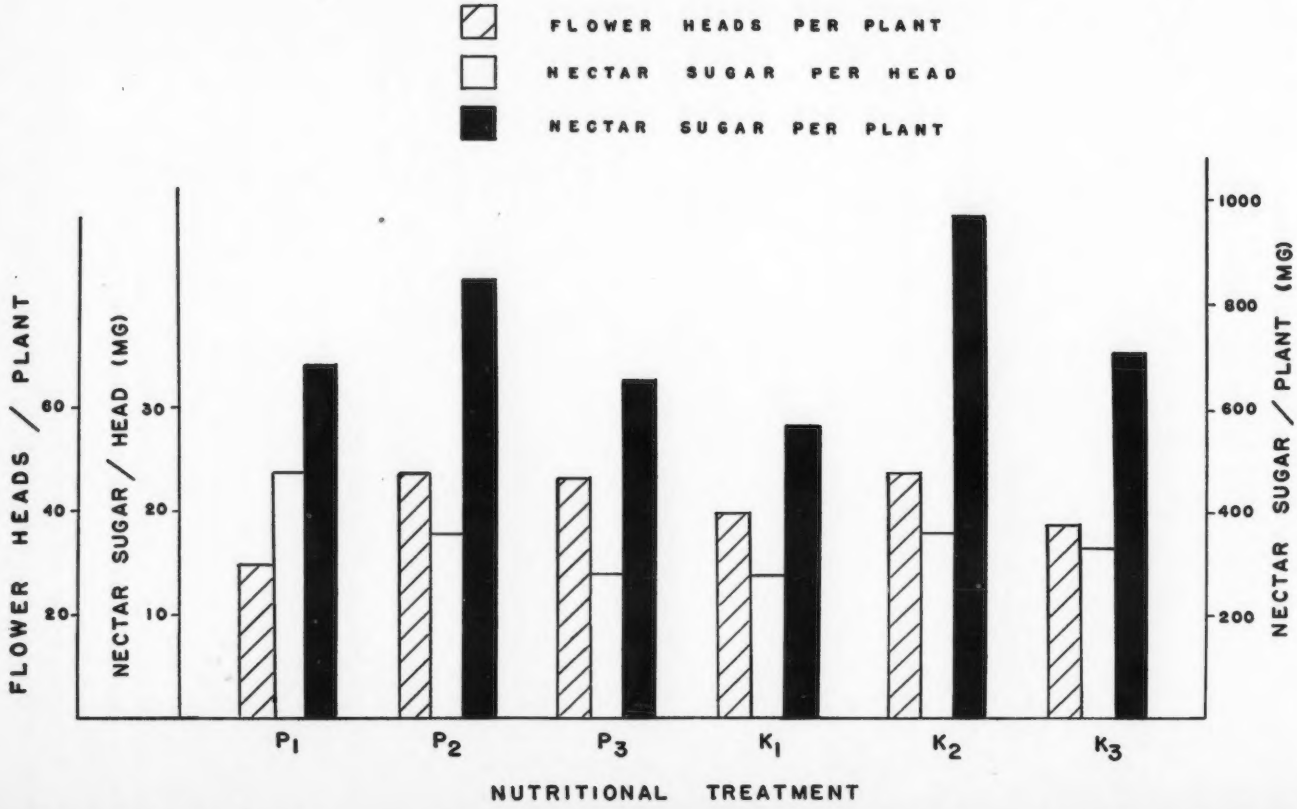

FIGURE 3. Average effects of phosphorus and potassium on nectar production in red clover. Standard errors of mean differences: for flower heads per plant, 3.4; for nectar sugar per head, 0.76 mg. for P_2 and P_3 comparisons, 0.93 mg. for all K comparisons. Standard error for nectar per plant not known.

TABLE 4.—PLANT GROWTH AND NECTAR SECRETION IN RED CLOVER AT THREE LEVELS EACH OF PHOSPHORUS AND POTASSIUM

Treatment	Mean oven-dry weight of plant tops	Mean number of flower heads per plant	Mean volume of nectar per 100 florets	Mean nectar sugar concentration	Mean weight of nectar sugar per 100 florets	Estimated weight of nectar sugar per plant
	g		μl	%	mg.	mg.
P_1K_1	43.5	32	21.40	67.8	19.43	575
P_1K_2	65.5	31	29.75	61.5	23.53	802
P_1K_3	70.5	24	28.70	62.4	23.56	630
P_2K_3 (Late)			29.30	60.8	23.34	
P_2K_1	41.5	33	23.35	49.7	14.70	483
P_2K_2	74.3	55	33.90	48.1	19.60	1031
P_2K_3 (Early)	83.0	51	38.30	45.1	20.62	966
P_3K_1	47.4	51	22.30	48.1	13.35	627
P_3K_2	50.0	53	29.20	48.7	17.11	859
P_3K_3	59.5	33	27.80	44.4	14.64	427
L S D $-P_1$ 0.05	12.4	11.9	2.41	1.4	2.74	
0.01	16.4	16.0	2.95	1.9	3.62	
$-P_2+P_3$ 0.05	12.4	11.9	4.50	2.2	2.59	
0.01	16.4	16.0	5.91	2.8	3.42	

L S D — Least Significant Difference

the P_2K_3 plants, flowering in the P_2 and P_3 groups had ceased by July 9. The P_1 group was a week later on the average, and was assayed for nectar in the period July 9-15. As nectar secretion is affected by weather conditions, secretion in the P_1 plants could not be compared directly with secretion in the P_2 and P_3 groups. Data from the P_1 groups were, therefore, analysed independently of the P_2 and P_3 data. Continuous flower production in the P_2K_3 plants over the whole sampling period did, however, permit an indirect comparison of early and late-flowering groups. The factor P_2K_3 (*early*)/P_2K_3 (*late*) was used to adjust nectar values in the P_1 treatments for such a comparison. Nectar data for the P_2K_3 treatment appear twice in Table 4, once for the early and once for the late part of the sampling period. In the graphs of Figure 3, no standard error is available for comparing P_1 treatments with P_2 and P_3 treatments.

Effects of Nutrition on Nectar Secretion

Data on the effects of the various PK combinations on secretion are presented in Table 4. Volume of nectar and weight of nectar sugar per head were substantially greater at the intermediate level of phosphorus than at the highest level. If nectar sugar weights for the P_1 treatments are adjusted for weather conditions by the factor mentioned above (approximately 0.9), weights of nectar sugar in the P_1 treatments are seen to compare favourably with those of the P_2 treatments.

The first increment of potassium led to a large increase in volume of nectar and weight of nectar sugar per 100 florets. The second increment produced an increase in volume only at the P_2 level, and this increase was cancelled out by a reduction in nectar concentration. At the highest

FIGURE 3. Average effects of phosphorus and potassium on nectar production in red clover. Standard errors of mean differences: for flower heads per plant, 3.4; for nectar sugar per head, 0.76 mg. for P_2 and P_3 comparisons, 0.93 mg. for all K comparisons. Standard error for nectar per plant not known.

concentration of phosphorus, the second potassium increment reduced the quantity of sugar secreted per 100 florets. Sugar concentration of nectar fell as the potassium supply was increased. More potassium was needed to produce this effect as the supply of phosphorus was increased.

The estimated yields of nectar sugar per plant appear in the last column of Table 4. The potential yield from the best combination of phosphorus and potassium, P_2K_2, was more than twice that of either of the poorest combinations, P_2K_1, and P_3K_3.

The general trends in nectar production per plant with variation in phosphorus and potassium concentration are illustrated in Figure 3. It is obvious that differences in flower production were just as important as variation in nectar secretion.

Potential plant yield of nectar was highest at the intermediate levels of both phosphorus and potassium. A deficit of phosphorus limited flower production, an excess reduced nectar secretion. The lowest concentration of potassium limited secretion, the highest concentration reduced flower production.

Relationship of Nectar Secretion to Weather Factors and Plant Development

Variation in secretion with weather was of the same order of magnitude as variation attributable to nutritional treatment. The range of daily sugar yields was from 14.6 to 25.4 mg. per 100 florets. Mean daily weights of nectar sugar were positively correlated with solar radiation during the 24-hour period preceding harvest ($r = +0.618$, significant at the 5 per cent level). Mean daily sugar concentrations of nectar were inversely correlated with average atmospheric vapour pressure for the same period ($r = -0.868$, significant at the 0.2 per cent level). The most interesting feature of the weather-secretion relationship was a treatment-weather interaction, but its nature was too obscure for interpretation.

Although secretion was not closely related to plant size, it was comparatively poor in the K_1 plants, whose growth was drastically limited by a deficit of potassium. This observation is in accordance with Ryle's results (12).

Quantity of nectar sugar per floret was related to head weight. Florets of large inflorescences generally secreted more nectar than those of small inflorescences ($r = +0.722$, significant at the 5 per cent level).

Nectar secretion did not appear to be related to the sugar content of the plant tissue, except in the intermediate-phosphorus treatments.

Staminal Tube Length and Pollination

Small quantities of nectar in long florets of red clover are often inaccessible to the honey bee. Dunham (6) has estimated that the average honey bee can reach through a distance of 7.9 mm. to extract nectar. In evaluating the influence of mineral nutrition on pollination of red clover, as it is mediated by nectar secretion, one should take into account the length of staminal tubes. It is conceivable that increases in quantity of nectar might be cancelled out by concurrent increases in staminal tube length. Florets in treatment P_2K_2, for example, yielded on the average

about 0.11 μl more nectar than those in treatment P_2K_1, but this increase was accompanied by an increase in staminal tube length of nearly 0.4 mm. In point of fact, it is unlikely that the longer florets would in this case have removed the nectar from the reach of a honey bee. The measured length of the staminal tube included the portion occupied by the ovary. The displacement of the ovary, coupled with the capillarly rise of nectar up the wall of the tube, should have brought the nectar to within easy reach of the tongue of the bee Goetze (7) has presented evidence that the bee is able to extract essentially all of the nectar from a red clover floret if it can reach the meniscus. If this is so, an increase in nectar sufficient to bring the nectar column to the threshold of availability should result in an addition to the nectar harvest greatly in excess of the nectar increment.

As the relationship of staminal tube length to phosphorus and potassium supply was complex, no generalizations can be made. Florets in the P_2K_1 and P_3K_1 treatments were about 0.25 mm. shorter than those in any other treatment. Stapel and Goetzache (18) found that fertilization with potassium increased floret length in red clover, whereas Ryle (12) found no such effect.

Possible Effects of Extraneous Elements on Secretion

In nutritional experiments encompassing wide variation in concentrations of certain elements, variation in other elements is unavoidable. The question arises of unsolicited effects on secretion of sodium, chlorine, and sulphur in the present experiments. These elements were present in excess of the needs of the plant in all treatments, and their variability was minor compared with that of the elements under investigation. Under such conditions one would expect their influence to be fairly uniform among treatments. Nevertheless, data on supply of sodium, chlorine, and sulphur were collated with nectar values for similar patterns of variation which might be interpreted as a cause-effect relationship. None was found for the red clover data. In the solutions supplied to the snapdragons, however, there was an inverse relationship between chlorine and nitrogen supply and a direct relationship between sulphur and potassium supply. The plant tissue was, therefore, analysed for chlorine and sulphur. It is obvious from the results of the analyses, which appear in Table 1, that any association between nectar values (Table 2) and tissue content of either chlorine or sulphur was negligible. The tissue content of these elements, in fact, bore no close relationship to their concentration in the mineral solution. It was therefore concluded that their effect on secretion was negligible. As the extreme variation in sodium concentration in the culture solution was less than 25 per cent, no sodium analyses were undertaken.

Although calcium and magnesium concentrations were uniform throughout each experiment, one might expect the sixteen-fold variation in potassium in the red clover experiment to be reflected in the calcium and magnesium content of the plant tissue. A relatively low content of calcium and magnesium might be expected in the P_3K_3 plants, which were exceptionally high in potassium (11, p. 437). The calcium and magnesium data in Table 3 indicate that such was the case. This factor may have

contributed to the poor nectar secretion in these plants. A comparison with calcium and magnesium contents of plants in the P_1K_2 treatment, which secreted abundantly, suggests that it was not very important.

Comparison between Species

Snapdragon and red clover may now be compared with respect to the most favourable levels of phosphorus and potassium for nectar secretion. The low levels of phosphorus supply were comparable in the two experiments (13 and 10 p.p.m., respectively), although the tissue content of phosphorus was higher in snapdragon (cf. Tables 1 and 3). This level of phosphorus was sub-optimal for flowering, but supported good secretion in both species. The P_2 treatments were roughly comparable in the two experiments with respect both to phosphorus supply (65 and 40 p.p.m. respectively) and phosphorus content of the plants. Flower production was abundant in both species in this range of phosphorus. Secretion was considerably reduced in snapdragon, but not, apparently, in red clover. Although the optimal level for secretion was lower than the optimum for flowering in both species, secretion appeared to be more sensitive to a high concentration of phosphorus in snapdragon.

The K_1 treatment in the snapdragon experiment (36 p.p.m.) may be compared with the K_2 treatment in the red clover experiment (45 p.p.m.) with respect to both external supply and tissue content of potassium. This level of supply limited growth in both species and promoted relatively good secretion in both. An increase in the potassium concentration of the mineral solution to 180 p.p.m. increased vegetative growth by about 43 per cent in snapdragon and 13 per cent in red clover. This higher concentration reduced nectar secretion decisively in snapdragon, but had no adverse effect on secretion in red clover, except when combined with the highest level of phosphorus. A concentration of potassium low enough to limit growth of red clover drastically (8 p.p.m.) was sub-optimal for secretion. It appears then, that secretion is favoured by a higher level of potassium in red clover than in snapdragon.

CONCLUSIONS

The following conclusions are drawn from the results of the two experiments:

1. Nectar secretion was affected by each of the elements studied. The nature of the individual effects on the physiology of secretion cannot be inferred from the present data. Reduction of secretion in snapdragon by a high concentration of nitrogen appears to have been associated with the effects of nitrogen on vegetative growth and tissue sugar content of the plant, as postulated earlier (15).
2. Nectar secretion in both snapdragon and red clover was apparently favoured by a supply of potassium less than that necessary for maximal growth, and a supply of phosphorus less than that necessary for maximal flower production. Secretion in snapdragon was more susceptible to reduction by a high concentration of potassium or

phosphorus than secretion in red clover. An abundant supply of potassium reduced sugar concentration of nectar in both species.

3. From the standpoint of the quantity of nectar produced by the whole plant, the effects of phosphorus and potassium on flowering were just as important as their effects on nectar secretion. Although specific fertilizer recommendations must await further information from field trials, the following general fertility conditions would appear to be desirable:
   (*a*) A level of nitrogen low enough to avoid excessively luxuriant growth.
   (*b*) A level of phosphorus which is sufficient to promote reasonably good flower production, but which is not high enough to reduce secretion.
   (*c*) A level of potassium which is neither low enough to limit growth drastically (and nectar secretion), nor high enough to inhibit flower production.
4. Variation in nectar secretion with nutritional treatment was of the same order of magnitude as the variation caused by weather factors in red clover, and of a somewhat lower order in snapdragon. Secretion may vary by a factor of several hundred per cent with solar radiation (14) and to a similar extent with genotype (10, 12). The influence of mineral nutrition on secretion, then, would appear to be of less importance than that of hereditary factors or weather conditions. When effects on both secretion and flower production are considered, however, nutritional control shows considerable promise as a method of increasing nectar flows and improving pollination.

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DOWNY MILDEW OF ONION AND ITS CONTROL IN THE BRITISH COLUMBIA INTERIOR[1]

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ABSTRACT

Downy mildew of onion appeared initially in the semi-arid British Columbia Interior about 50 years after onion crops had been first grown commercially. The year of its appearance, 1942, was abnormally wet, and this condition suggested that the weather had previously been unfavourable for its establishment. However, the disease has since persisted and has caused damage in most seasons. The pathogen was probably present on infected living plants introduced shortly before the appearance of the disease.

Systemic overwintering of the pathogen in diseased bulbs occurs only occasionally. Heat treatment of seed mother bulbs was found to injure them sufficiently to seriously reduce the number and height of seed stalks.

Zineb provided best control in fall-planted, spring-planted, and seed crop onions. Maneb and ferbam were less effective. Captan and NP–1282 were ineffective. Control was found to be effective only if a spray was applied at first indication of mildew in a district.

INTRODUCTION

The relatively recent appearance of downy mildew of onion (*Peronospora destructor* (Berk.) Caspary) in the semi-arid sections of the British Columbia Interior has provided an opportunity for interesting observations on the epidemiology of this disease. It has also necessitated a search for satisfactory methods of control.

Onion crops have been grown in these irrigated districts since the end of the last century. The weather and the soils of this area are well suited to commercial production of this vegetable.

In early years, production was confined to commercial crops of spring-planted onions. These have been mostly of the yellow types, such as Yellow Globe Danvers and Ebenezer. There have been limited plantings of White Portugal, but the red varieties have seldom been grown. A more recent development has been the growing of onions for seed. Seed crops of the yellow, red, and white types grow well, and large yields per acre are usually secured. Another development has been commercial production of fall-planted onions of the Sweet Spanish type. Formerly all young plants were imported from eastern Washington, but local production in the Okanagan Valley has been started.

EPIDEMIOLOGY

History of the Disease in the British Columbia Interior

Downy mildew has a relatively short history in these plantings. For about 50 years the only diseases that were known to affect onion crops in the region were bulb rot (*Fusarium oxysporum*) (Schlect.) forma *cepae* Snyder and Hansen), and neck rot (*Botrytis allii* Munn.). In 1942 downy

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mildew was observed for the first time in two districts of the British Columbia Interior. McLarty (1) reported its occurrence in the "*Canadian Plant Disease Survey*" as follows: "Downy mildew was found affecting all the plants at Armstrong and fully 50% of the crop at Vernon. The disease was present at Kelowna, but not quite so prevalent. In general, the loss was about half the crop. This is the first time that the disease has been recorded in the Okanagan Valley".

The following year mildew was found at Grand Forks, the principal centre for onion seed production in the province. Most of the onion seed crop was severely affected. Every year since, the disease has been found in all these localities although the extent of damage has varied in different seasons. Occasionally the damage has been negligible, but in most years mildew has caused moderate to severe economic losses. The disease has not yet been found in the Kamloops area.

Prior to its discovery in the interior districts, onion mildew had occurred for many years in the more humid coastal areas of the province, where damage was confined mostly to seed crops.

It is not known how mildew became established in the interior of the province after so many years of freedom. In 1942, when the disease first occurred in the Armstrong and Vernon districts, summer rains were more than normally frequent. For the four growing months, May to September, total rainfall was 12.00 inches in Armstrong and 12.37 inches in Vernon. Average rainfall for this period was 5.47 inches and 5.21 inches respectively. This climatic circumstance aroused the suspicion that the fungus had been present in the region for many years, that it had been persisting in unobtrusive infections of host plants growing in especially favourable locations, and that during the wet weather of 1942 it had increased in prevalence sufficiently to cause damage. However, persistence of the disease each year since 1942 has suggested that normal weather in the region allows mildew to cause damage in most seasons. It seems more probable that the British Columbia Interior was free of the mildew pathogen until 1942, and that it was introduced in that year, or one of the years immediately preceding, on infected living plants imported into the region for commercial field planting. The unusually wet 1942 summer weather presumably assisted in the establishment of the pathogen.

Systemic Infection

An experiment was conducted at Kelowna, B.C., in 1949, to determine whether, under conditions in the British Columbia Interior, the mildew pathogen overwinters in the bulbs. A one acre field was planted with mother bulbs, all of which had become mildewed the previous season. Only six plants out of several thousand showed any symptoms of mildew. This infection was found on May 23, when the plants were about 18 inches high. Affected plants were stunted. The leaves were reflexed instead of being nearly upright as in healthy plants, and they were a slightly lighter green than normal. Some sporulation occurred on the foliage. In similar examinations at Grand Forks, B.C., no systemic infection was

found in any of several commercial fields planted with mother bulbs that had been severely mildewed the previous season. From these results it is apparent that systemic overwintering of onion mildew in diseased bulbs is possible in the British Columbia Interior. However, the rate of infection is very small and it seems probable that systemic infection in onion plays an extremely minor role in overwintering of the pathogen. Yarwood (2) has observed similar results under California conditions.

EXPERIMENTS ON DISEASE CONTROL

Heat Treatment of Bulbs

Field experiments were carried out in 1949 at Kelowna to explore the possibilities of heat treatment similar to that described by Yarwood (2). Plants were grown from Yellow Globe Danvers bulbs that had been treated previously (a) at the end of March by the dry heat method at a constant air temperature of 42°C. (107.6°F.) for 17½ hours; and (b) at the middle of April, just prior to field planting, by the wet heat method at a constant water temperature of 45°C. (113°F.) for 1¼ hours. At the end of June, 202 flower stalks with an average height of 31.5 inches had developed on 75 untreated check bulbs; 126 flower stalks with an average height of 27.0 inches on 75 bulbs treated with dry heat; and 62 flower stalks with an average height of 20.0 inches on 75 bulbs treated with wet heat. No mildew developed on any of the plants, including the checks. However, the results did demonstrate that heat treatment is risky at the temperatures and hours of treatment used, and may reduce the number and height of the seed stalks.

Spray Trials

During 1953, 1954, and 1955, several spray materials were applied experimentally to fall- and spring-planted onions growing in the section of the Kelowna district where mildew has caused damage most frequently.

The waxy surface of onion foliage renders it much more difficult to wet with spray materials than that of most other plants. Many wetting agents that ensure good spray coverage on plants having non-waxy foliage are practically useless on onion. Sodium lauryl sulphate, in such household detergents as "Vel" and "Dreft", has proved an excellent wetting agent for sprays being applied to onions. "Vel" was incorporated in all the sprays, with satisfactory results, at the rate of 1 lb. to 100 Imperial gal. of water in 1953, and ½ lb. to 100 gal. in 1954 and 1955.

(a) 1953 Tests

Six weekly applications were made on each of two replicates of fall-planted onions of the Sweet Spanish type. The first spray was applied on June 9, before mildew had appeared in the experimental plots but soon after the first signs of mildew had appeared in the district. Two fungicide preparations containing zineb and ferbam were each applied at the rate of 2 lb. to 100 Imperial gal. of water by means of a portable Hardie sprayer at a pressure of about 250 lb. The third material, NP–1282 (50% pentachlorophenolmercaptoacetic acid)*, was in short supply and was applied

*Supplied by Pennsylvania Salt Manufacturing Company of Washington, Tacoma, Wash.

TABLE 1.—CONTROL OF ONION MILDEW IN 1953: EFFECT OF TREATMENT ON LEVEL OF INFECTION IN PLOTS OF SPRING-PLANTED ONIONS

Fungicide preparation	Amount per 100 gallons water	Average percentage of plants showing foliage infection		
		None	Slight	Severe
Zineb	2 lb.	98.5	1.5	0.0
Check	—	52.0	35.0	13.0
Ferbam	2 lb.	72.5	22.0	5.5
Check	—	34.0	41.5	24.5
NP–1282	5 lb.	73.0	23.0	4.0
Check	—	46.0	30.0	24.0

five times to a much smaller plot with a knapsack sprayer, diluted at the rate of 5 lb. to 100 gal. of water. Approximately one-half of the spray mixture was applied along the rows in one direction, and the remainder in the opposite direction, in order to assure as complete a spray coverage as possible.

Data on control (Table 1) were secured just prior to harvest by examining every fifth plant until a total of 100 plants had been reached. Counts from the two replicates were averaged, and the bulbs classified into three groups according to the level of infection, as follows:

Infection none—foliage apparently free of mildew.
Infection slight—mildew infection at or near the tips of some of the leaves.
Infection severe—most of the foliage killed or severely affected by mildew.

Zineb was the most effective of the three materials used. Of the plants sprayed with this preparation, 98.5 per cent were free of mildew, in contrast to 72.5 and 73 per cent clean plants in plots sprayed with ferbam and NP–1282. Of the unsprayed check plants, 34 to 52 per cent remained free of mildew, which indicated that the disease was only moderately severe in 1953.

(b) 1954 Tests

Experiments were conducted in small plots located in three separate parts of the field. They were applied first to fall-planted onions of the Sweet Spanish type, and later in the season to spring-planted Yellow Globe Danvers onions. The sprays were applied with a knapsack sprayer at 10-day intervals. For the spray mixtures, to each 100 gal. of water, fungicide preparations were added in the following amounts: zineb, 2 lb.; ferbam, 2 lb.; NP–1282, 6 lb.; captan, 2 lb.; maneb, 2 lb.

The fall-planted onions received five applications. The first spray was applied on June 3. No mildew was found until the time of the fourth spray, July 5, when a trace of mildew was evident on unsprayed plants. However, on July 15, when the final spray was applied, mildew was quite prevalent on unsprayed plants in one section of the field. As the disease

TABLE 2.—CONTROL OF ONION MILDEW IN 1954: EFFECT OF TREATMENT ON INFECTION AND ON YIELD IN PLOTS OF FALL-PLANTED ONIONS

Fungicide preparation	Amount per 100 gallons water	Average percentage of plants showing foliage infection			Weight of 300 bulbs (lb.)	Percentage increase in bulb weight
		None	Slight	Severe		
Check (no spray)	—	0.0	0.0	100.0	125.0	—
Zineb	2 lb.	90.3	9.7	0.0	217.0	73.6
Maneb	2 lb.	8.3	89.4	2.3	165.0	32.0
Ferbam	2 lb.	0.0	60.0	40.0	178.5	42.8
Captan	2 lb.	0.0	19.3	80.7	136.5	9.2
NP–1282	6 lb.	0.0	0.0	100.0	133.0	6.4

failed to develop on the other replicates, the effect of the treatments on infection and yield was recorded from the single replicate located in this section of the field.

Shortly before harvest, a record was made of leaf mildew infection by examining 100 plants in each of three parts of each plot. These were grouped as in 1953. Results are shown in Table 2.

The practical value of mildew control lies in the increase of crop yield. Accordingly, samples of 300 bulbs were collected in three different locations in each plot. A record was made of the combined weight of bulbs and tops, and the percentage increase in weight over that of samples from the unsprayed checks was calculated (Table 2).

Spring-planted Yellow Globe Danvers onions were sprayed four times at 10-day intervals. The same five fungicides used in the earlier sprays were employed in the first application. This was during the last week in July, immediately after the first trace of mildew infection had been detected in the locality on this crop and just before final results were secured on the fall-planted onions. Because captan and NP–1282 were ineffective in checking the disease on the fall-planted onions, it was considered useless to use them further and they were replaced with zineb in the three remaining sprays.

Data on disease control were secured at harvest in September, and again included the effect of the sprays on both leaf infection and crop yield. These are shown in Table 3.

(c) 1955 Tests

Commercial onion seed crops of the variety Ebenezer were sprayed four times at 10-day intervals during late June and early July. Three plots, each one-third acre in size and located on different farms, were sprayed with zineb at the rate of 4 lb. to 100 gal. DDT, at the same rate, was incorporated in the last three sprays for onion thrip control. The sprays were applied with a high volume dilute sprayer operating at 500-lb. pressure and applying sprays at the rate of 400 gal. per acre. Mildew did not appear until the last week of July, and developed in only one plot.

TABLE 3.—CONTROL OF ONION MILDEW IN 1954: EFFECT OF TREATMENT ON INFECTION AND ON YIELD IN PLOTS OF SPRING-PLANTED ONIONS

Fungicide preparation	Amount per 100 gallons water	Average percentage of plants showing foliage infection			Weight of 300 bulbs (lb.)	Percentage increase in bulb weight
		None	Slight	Severe		
Check (no spray)	—	0.0	0.0	100.0	63.8	—
Zineb	2 lb.	47.7	41.5	10.8	81.8	28.2
Maneb	2 lb.	3.8	56.7	39.5	85.2	33.5
Ferbam	2 lb.	0.2	13.5	86.3	73.8	15.7
Zineb (Captan in 1st spray)	2 lb.	0.7	19.5	79.8	75.3	18.0
Zineb (NP–1282 in 1st spray)	2 lb.	0.0	13.2	86.8	70.7	10.8
Difference required (P = .05)					23.8	

TABLE 4.—CONTROL OF ONION MILDEW IN 1955: EFFECT OF TREATMENT ON SEED STALK INFECTION

Fungicide preparation	Amount per 100 gallons water	Number of stalks counted	Average percentage of stalks showing infection		
			None	Slight	Severe
Zineb	4 lb.	1000	90.9	7.9	1.2
Check (no sprays)	—	1020	39.9	25.7	34.4

Disease control in the affected plot was assessed shortly before harvest by examining 100 seed stalks in each of ten different parts of the plot (Table 4). The stalks were classified in three groups, as follows:

Infection none—apparently free of mildew infection.

Infection slight—slight mildew infection at one or more positions on seed stalk; affected tissues green and apparently still functioning.

Infection severe—tissues of one or more lesions killed by mildew and usually black, following secondary fungus infection.

The differences were more apparent than the table indicates, because in the unsprayed check plot the lesions found on stalks having severe infection were quite numerous, were usually large, and were necrotic. The stalks were severely injured, weak, and often falling over. On the other hand, in the sprayed plot lesions were much less numerous, usually only one per stalk, and were small. Although the affected tissues were black and dead, the stalks appeared to suffer very little injury and remained upright.

In addition, fall- and spring-planted onions were treated in the same location as, and in a manner similar to, the control experiments carried out in 1953 and 1954. The low level of mildew infection in the district precluded assessment of control results but an opportunity was provided

to determine whether any or all of the spray materials might have an effect on bulb size, apart from disease control. Data on crop yields were secured, similar to those obtained in 1954. There was no significant difference in yields between any of the sprayed and check plots.

DISCUSSION OF SPRAY RESULTS

The year 1954 provided the most satisfactory results in both fall-planted and spring-planted crops. In both crops zineb was the most effective fungicide in reducing foliar infection. Its effectiveness was especially evident in the fall-planted crop, for which it protected 90.3 per cent of the leaves from infection, whereas the unsprayed checks in the same plot suffered 100 per cent severely affected leaves. None of the other materials provided satisfactory protection, although maneb and ferbam gave a measure of control. For the spring-planted crop, zineb provided only 47.75 per cent of leaves completely free of infection, compared to 100 per cent on unsprayed checks, but its effectiveness was much greater than that of the other materials tested.

The most marked increase in bulb size resulted from zineb treatment of fall-planted onions. Unfortunately the presence of mildew, and therefore the availability of results, in only one of the replicated plots precluded statistical analysis of these results. In the spring-planted crop, in which all plots developed some degree of mildew infection, the average increase of bulb size was considerably less, and the F value was 3.09 (with 3.3 required at $P = 0.05$). The percentage increase varied widely from plot to plot. Because the tests were conducted in a commercial onion field where cultural conditions were not uniform there appears justification for attributing the variability to : (a) differences in soil tilth between plots due to some irrigation puddling; and (b) inconsistent plant thinning, with bulbs in some plots growing so closely that they were not able to size properly.

The 1953 and 1955 results provide additional evidence of the effectiveness of zineb in controlling leaf infections. Whenever mildew was serious in a crop the foliage of plants that had been sprayed with zineb was still green and functioning when the crop was ready to harvest; and the same condition was found in decreasing degrees in plots treated with maneb and ferbam. In contrast, the foliage of unsprayed plants or those treated with the ineffectual fungicides captan and NP–1282, was dead, brown, and dry when the bulbs were harvested. The increase in bulb size over unsprayed that was recorded for all sprayed plots in 1954 presumably resulted from the longer and more efficient functioning of the foliage. The lack of marked differences in crop yields between sprayed and unsprayed plots in 1955, when mildew infection was mild, substantiates this conclusion.

These experiments have indicated that zineb is the fungicide that should be recommended for onion downy mildew control in the British Columbia Interior. Maneb and ferbam could be considered as less satisfactory substitutes.

The importance of correct timing of sprays was demonstrated in the 1954 results (Table 3). Zineb applied in later sprays, following a first spray of a less effective fungicide, gave a low degree of control that contrasted with the efficiency of the full zineb program. Application of a spray at first indication of mildew infection in a district appears to be critical.

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THE EFFECT OF NITROGEN, PHOSPHORUS AND POTASSIUM ON LODGING IN OATS[1]

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ABSTRACT

Studies under both greenhouse and field conditions have been conducted to determine the effects of nitrogen, phosphorus, and potassium on lodging of oats. Resistance to lodging in oats is influenced to an important degree by the development of culm, coronal root system, and plant height. The effects of nitrogen, phosphorus, and potassium on the three characters were measured and combined into single lodging index value in order to determine the complete effect of treatment on lodging.

Phosphorus improved lodging resistance to an important degree. Nitrogen increased lodging susceptibility, except when it was combined with phosphorus. Potassium, alone, improved lodging resistance but was not effective when applied with either phosphorus or nitrogen. The greatest resistance to lodging was provided by a combination of nitrogen, phosphorus, and potassium.

INTRODUCTION

Lodging prior to maturity is one of the serious hazards which must be considered in any fertility program designed to produce high oat yields. Of the types of lodging encountered, lodging prior to maturity, caused by poor culms and plant anchorage, is the most common. In oats, it has been established by Hamilton (2, 8, 9) that resistance to lodging prior to maturity depends largely on the development of the culm, and coronal roots in the top 6 inches of soil. Resistance to lodging is provided by a large, strong culm and stiff, spreading coronal roots which resist being uprooted. A third factor which affects lodging is plant height.

The objective of this study was to investigate the effects of chemical fertilizers on the three plant characters associated with lodging resistance of oats. The effects of each treatment are combined into a single value designated by Hamilton (8, 9) as the lodging index. This is a new approach. Previous workers (1, 3, 7,) have assessed the effects of fertilizer treatments on lodging by means of field appraisement. Where the effects of fertilizer treatment on roots were evaluated, (4, 5, 10, 11, 12, 14), the entire root system was considered and not the culm and coronal root portion in the top 6 inches of soil.

MATERIALS AND PROCEDURE

The varieties used were Ardri, Beaver, and Dasix, which may be rated on the basis of field performance as having strong, medium, and weak resistance to lodging, respectively.

[1] Contribution from the Illustration Stations Division, Experimental Farms Service, based on thesis submitted to the School of Graduate Studies, McGill University, in partial fulfilment of requirements for the degree of M. Sc.

The fertilizer materials were ammonium sulphate, superphosphate and muriate of potash. The treatments follow:—

(O)	Check—no fertilizer
P	100 lb. phosphoric acid
K	75 lb. potash
PK	100 lb. phosphoric acid plus 75 lb. potash
N	60 lb. nitrogen
NP	60 lb. nitrogen plus 100 lb. phosphoric acid
NK	60 lb. nitrogen plus 75 lb. potash
NPK	60 lb. nitrogen plus 100 lb. phosphoric acid plus 75 lb. potash.

In the greenhouse experiments a Castor fine sandy loam was used, a soil low in available nitrogen, phosphorus and potash. Eight treatments, in duplicate, were applied to respective pots in which Ardri and Dasix were seeded. Pots were arranged in randomized design.

In field studies, carried out for a 3-year period on a Grenville sandy loam, a soil type rather similar to Castor, a split-plot design was used with the three varieties Ardri, Beaver, and Dasix, as main plots and treatments randomized within varieties as sub-plots. Three replications were carried each year. Plant height data were recorded on all material. Culm diameters were taken 1 inch above soil level with a micrometer caliper. Root types were classified according to a scale of values established by Hamilton (8, 9). This is a 1-10 scale, progressing from 1, which represents rigid, spreading coronal roots and good basal culm development, to 10, which represents a poorly-developed, weak coronal root system and basal culm.

In order to assess the total effect of treatment on lodging, the combined effect of treatment on plant height, root type, and culm size must be cumulated into a single value. In lodging resistance, plant height is a negative factor. An increase in height decreases lodging resistance.

In lodging studies by Hamilton (8, 9) the discriminant function analysis method (6) was used to evaluate the proportionate contribution of each plant character to lodging resistance. The average discriminant function values established by Hamilton were used in the present study. The relative ratio of the importance of the plant characters, culm diameter, root type, and plant height was established as 10:5:1. By means of this method, it was possible to combine the effects of each treatment on the three characters associated with lodging resistance into a single value.

RESULTS AND DISCUSSION

In lodging resistance, the characters influencing lodging in ascending order of importance are plant height, root type, and culm diameter (8, 9). The effects of each treatment on these plant characters both under greenhouse and field conditions are first examined.

Plant Height

Nitrogen consistently increased plant height as shown in Figures 2 and 3. The average increase for all nitrogen treatments was 6.3 inches

FIGURE 1. The effect of treatment on root rot type and culm development.

No. 1	(O) Check	No. 5	N
No. 2	P	No. 6	NP
No. 3	K	No. 7	NK
No. 4	PK	No. 8	NPK

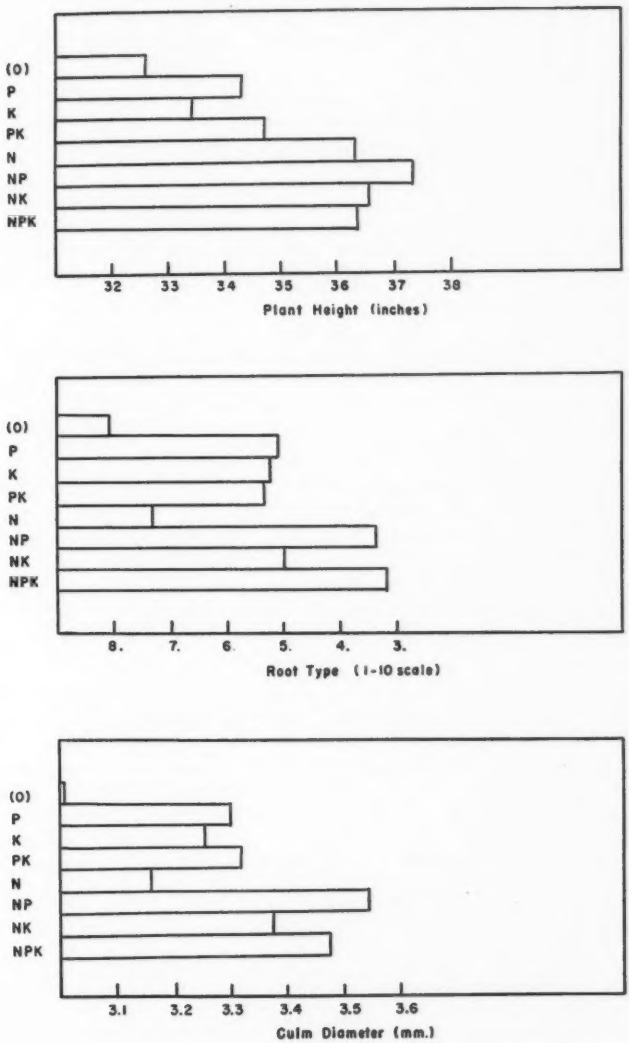

FIGURE 2. The effect of fertilizer treatments on plant height (inches), root type (1-10 scale), and culm diameter (mm.) under greenhouse conditions.

under greenhouse conditions and 2.9 inches in field studies. Phosphorus also increased height but to a lesser degree, this increase being 2.2 inches in the greenhouse and 1.0 inch under field studies. Potash increased plant height in the greenhouse but was not consistently effective in the field.

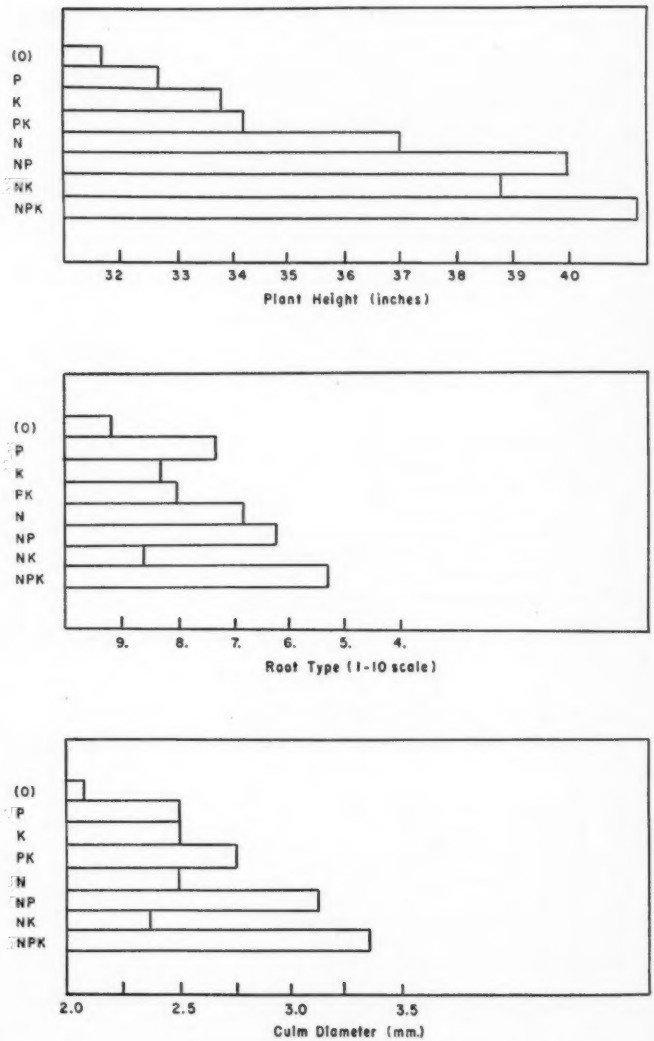

FIGURE 3. The effect of fertilizer treatments on plant height (inches), root type (1-10 scale), and culm diameter (mm.) under field conditions.

Root Type

Nitrogen, phosphorus and potash each improved root type when applied singly, with phosphorus causing the greatest improvement. Phosphorus was more effective when applied with nitrogen. The effects of treatment on root type are illustrated in Figure 1. Figure 1 was prepared from sample roots grown under treatment in the greenhouse.

Figures 2 and 3 illustrate the total effects of treatments on root type under greenhouse and field conditions.

Culm Diameter

The effect of treatment on culm diameter was quite similar to that caused on root type. Phosphorus caused the greatest improvement.

Lodging Index Values

The lodging index value, developed from the 10:5:1 relationship of culm diameter, root type and plant height, increases with decreases in lodging resistance. The lodging index gives a relative effect of the various treatments on lodging resistance of oats. The lodging index values obtained under greenhouse conditions as well as increase in resistance due to treatment on Ardri and Dasix are presented in Table 1. Similar data under field conditions, for the varieties Ardri, Beaver and Dasix, summarized for a 3-year period, are presented in Table 2. It is noteworthy that phosphorus alone and in combination produced positive effects on lodging resistance, with N P K lowering the index value most. The effect of potash was more variable. It was effective with Ardri but less efficient with Dasix. The negative effect of nitrogen is explained by the fact that this element influenced plant height to a much greater degree than it influenced root type and culm diameter. In the preliminary study under discussion it was impossible to correlate actual lodging data with fertilizer treatment. Lodging is prevented under greenhouse conditions, and in the field studies no lodging took place on the experimental area.

Further work is at present under way to ascertain the most effective levels at which to combine nitrogen, phosphorus and potash. This work

TABLE 1.—LODGING INDEX VALUES AND IMPROVEMENT DUE TO TREATMENTS FOR TWO VARIETIES—GREENHOUSE EXPERIMENT

Treatment	Ardri		Dasix		Average	
	(1)	(2)	(1)	(2)	(1)	(2)
(1)	52.3	—	57.0	—	54.7	—
P	39.5	12.8	45.9	11.1	42.7	12.0
K	41.2	11.1	56.2	0.8	48.7	6.0
PK	49.6	2.7	46.8	10.2	48.2	6.5
N	49.5	2.8	61.2	−4.2	55.4	−0.7
NP	37.0	15.3	42.7	14.3	39.9	14.8
NK	49.7	2.6	61.9	−4.9	55.8	−1.1
NPK	31.8	20.5	38.0	19.0	34.9	19.8

(1) Lodging index value.
(2) Increase in lodging resistance.

TABLE 2.—LODGING INDEX VALUES AND IMPROVEMENT DUE TO TREATMENTS FOR THREE VARIETIES—FIELD EXPERIMENT

Treatment	Ardri		Beaver		Dasix		Average	
	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)
(1)	38.4	—	43.4	—	39.5	—	40.4	—
P	25.3	13.1	38.7	4.7	31.7	7.8	31.9	8.5
K	26.5	11.9	32.6	10.8	36.2	3.3	31.8	8.6
PK	29.0	9.4	33.8	9.6	36.2	3.3	33.0	7.4
N	36.0	2.4	43.6	−0.2	43.9	−4.4	41.2	−0.8
NP	22.5	15.9	32.8	10.6	31.0	8.5	28.8	11.6
NK	27.5	10.9	33.7	9.7	36.9	2.6	32.7	7.7
NPK	19.4	19.0	29.5	13.9	33.8	5.7	27.6	12.8

(1) Lodging index value.
(2) Increase in lodging resistance.

will include a study of the correlation of lodging index value changes as affected by varying fertilizer levels and the actual lodging resulting under field conditions.

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FURTHER EXPERIMENTS ON CONTROL OF THE ONION MAGGOT, *HYLEMYA ANTIQUA* (MG.), IN THE INTERIOR OF BRITISH COLUMBIA[1]

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ABSTRACT

Experiments at two localities in the interior of British Columbia in 1952 and 1953 showed that a seed treatment of dieldrin at 0.5 oz. per pound of seed gave as good control of the onion maggot as any other treatment, was not phytotoxic, and gave the highest yield of marketable onions each year. Lindane, 25 per cent wettable powder, applied three times at 10-day intervals to the soil surface at 1 lb. of toxicant per acre per application gave consistently good control and high yields, but was more expensive in both labour and materials. Calomel at 1 lb. per pound of seed gave satisfactory control in a light infestation but cost twenty times as much as dieldrin. DDT at 8 oz. per pound of seed gave effective control but the bulk of insecticide on the seed caused jamming of the seeder. When the amount of DDT was reduced the degree of damage increased. Lindane as a seed treatment at 1 oz. per pound of seed was extremely phytotoxic. The same amount of aldrin applied in a similar manner was phytotoxic but to a lesser degree.

INTRODUCTION

Experiments in the interior of British Columbia in 1950 and 1951 [Finlayson and Handford (4)] showed that DDT was a practical and relatively inexpensive substitute for calomel as a seed treatment to control the onion maggot, *Hylemya antiqua* (Mg.). Unfortunately, the amount of DDT necessary for satisfactory control caused an irregular flow of seed even when the outlet of the seeder was opened more than normally. Consequently some growers reduced the amount of DDT but found that the degree of protection was lowered. The same experiments indicated that aldrin and dieldrin at reduced amounts would give practical control. This is a report on experiments at Kelowna and Vernon, B.C., in 1952 and 1953 respectively, designed to determine the amounts of these and other insecticides necessary for practical control and the effects these amounts had on seedling emergence, plant growth, and yield of marketable onions.

METHODS AND MATERIALS

The methods were adapted from those used by McLeod (7) and Finlayson and Handford (4).

The plots at both sites were arranged in randomized blocks replicated four times. Each plot had five rows, 25 feet long, with 16 inches between rows, the outside rows serving as buffers. In 1952 there were nine treatments; in 1953, fourteen.

All seeding was done with a rod-row multiple-gear seeder. The variety Yellow Globe Danvers No. 55 was used.

[1]Contribution No. 3401, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada; in part from a thesis to be submitted to the University of Western Ontario in partial fulfilment of the requirements for the Ph.D. degree.

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TABLE 1.—TOXICANT PER POUND OF SEED AND AVERAGE NUMBER OF SEEDLINGS EMERGED IN TREATMENTS AGAINST THE ONION MAGGOT AT KELOWNA, B.C., 1952, AND VERNON, B.C., 1953[1]

Kelowna				Vernon		
Treatment	Toxicant oz./lb. of seed[2]	Seedlings	Square root transformation[3]	Treatment	Toxicant oz./lb. of seed[2]	Seedlings[3]
Aldrin, 50%[4]	1.0	267	16.29	Lindane, 25%[5]	1.0	731
DDT, 50%[5]	8.0	326	17.87	Aldrin, 25%[6]	1.0	858
Dieldrin, 50%[4]	0.1	354	18.72	Aldrin, 25%[6]	0.5	926
Check	—	364	18.87	Dieldrin, 50%[4]	1.0	970
Dieldrin, 50%[4]	1.0	362	18.95	Lindane, 25%[5]	48.0	1011
Dieldrin, 50%[4]	0.5	372	19.14	Dieldrin, 50%[4]	0.5	1046
DDT, 50%[5]	2.0	393	19.78	Check 1[8]	—	1062
Calomel[7]	16.0	404	19.99	DDT, 50%[5]	8.0	1070
Lindane, 25%[5]	48.0	453	21.06	Dieldrin, 50%[4]	0.1	1086
				DDT, 50%[5]	1.0	1086
				Aldrin, 25%[6]	0.1	1102
				DDT, 50%[5]	2.0	1110
				Calomel[7]	16.0	1114
				Check 2[8]	—	1124

[1]Rate of seeding per acre: 5 lb.
[2]Lindane at 48 oz. is a surface treatment and the amount is per acre; all others, seed treatments.
[3]Any two means within the same bracket are not significantly different; any two not within the same bracket are significantly different [Duncan (1)].
[4]Wettable powders prepared from crystalline forms and supplied for experimental purposes, Julius Hyman and Co., Denver, Colo.
[5]Wettable powder prepared from crystalline forms; [6]Wettable powder prepared by spraying a 60 per cent soluble aldrin plus 40 per cent reaction products on to an inert carrier; and [7]Technical powder containing 99 per cent mercurous chloride, Ansell Laboratories, Vernon, B.C.
[8]See "Methods".

The insecticides tested were: aldrin, calomel, DDT, dieldrin, and lindane. The formulations, sources, and amounts are shown in Table 1, the amounts being based on previous experiments [Finlayson and Handford (4)] and comparative toxicities. Lindane at 48 oz. per acre was applied as a surface treatment; all of the others were seed treatments.

Seed treatments were effected by moistening the seeds with water and mixing the moistened seeds with a specific amount of chemical until it adhered uniformly to the seed [Glasgow (5)]. When the application was 0.1 oz. of toxicant per pound of seed, ten times the amount of chemical necessary was mixed into a suspension with ten times the amount of water necessary to moisten the seed, and one-tenth of this suspension was applied to the seed.

For the surface treatment, lindane was mixed with water and applied to the seedlings and soil surface at 1 lb. of toxicant in 260 gallons of water per acre per application. Three applications were made, the first when approximately 50 per cent of the seedlings were in the loop stage; i.e., just before the cotyledon became free of the ground, and the second and third at 10-day intervals.

In 1952, only seeds being seed-treated were moistened with water and only plots being surface-treated received additional water after germination. In 1953, all seed for sowing was moistened with water, to compensate for any advantage that pre-seeding moistening might have on germination, and all plots except Check 1 received water at 260 gallons per acre per application at the same time the surface treatment was applied; this compensated for any undue influence the added moisture might have on oviposition of the flies or on plant growth.

Phytotoxic effects of the insecticides were measured by counting the plants when they emerged and by observing symptoms in the aerial parts of the plants.

Maggot damage was appraised at 5-day intervals from emergence of the seedlings to the end of June and at weekly intervals from then until harvest. The damaged plants, identified by the wilting leaves, were pulled, the cause of damage was determined, and the plants were placed on the ground as close as possible to the spots from which they were uprooted. They were not replanted. Thus the maggots could inflict a degree of damage approximating what would have occurred if the damaged onions had not been pulled for examination. An additional count of damaged plants was made when the onions were thinned, about four weeks after the seedlings emerged. Percentage damage was calculated from the total number of damaged plants in terms of the number of emerged seedlings.

Yield of marketable onions measured the combined effects of phytotoxicity and maggot damage and possibly other factors. The normal practice of thinning was completed at both sites.

All records were made from the three central rows of each plot.

To determine the effects of the seed treatments on germination, four replicates of 25 seeds for each treatment were placed in closed petri dishes on two thicknesses of moist filter paper in a rearing cabinet at 75° F. and 70 per cent R.H. Water was added when needed.

Data* on germination, emergence, damage, and yield were examined by analysis of variance and the multiple range test [Duncan (1)].

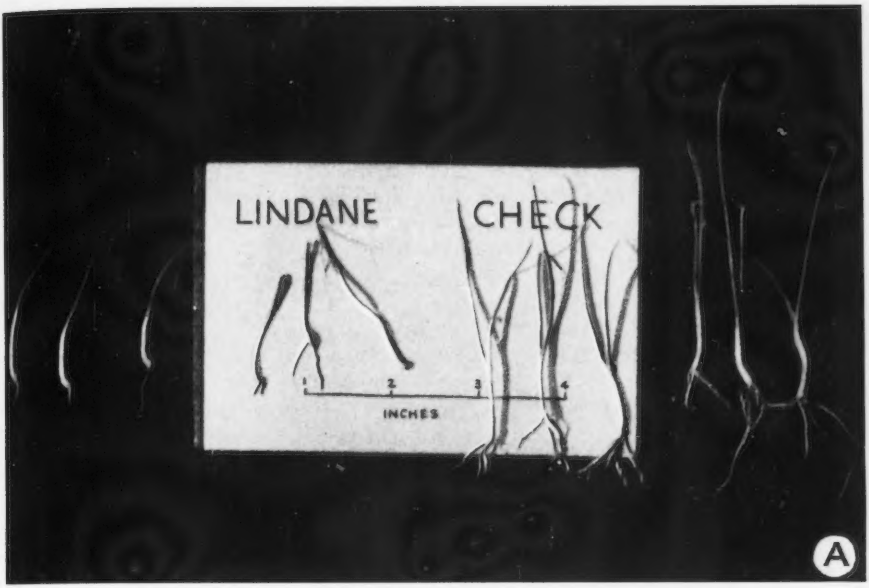
RESULTS

The various treatments at both localities caused significant differences in emergence, maggot damage, and yield of marketable onions (Tables 1-3).

Table 1 shows that at Kelowna in 1952 only the seed treatment with aldrin gave significantly fewer seedlings than the check; at Vernon, in 1953, the three seed treatments with aldrin at 0.5 and 1.0 oz. per pound of seed and lindane at 1 oz., produced significantly fewer seedlings than either check. The number of seedlings for the lindane treatment was significantly lower than those for any of the other treatments.

In addition to the reduced number of seedlings grown from seed treated with lindane and aldrin in 1953, definite phytotoxic symptoms were present as early as the flag stage of the seedlings; i.e., when the cotyledon becomes free of the ground and passes through the angle of 180

*An examination of the treatment means and variances revealed no regular pattern in those for seedling emergence in 1953 and yields for 1952 and 1953; and hence it is safe in general to use untransformed data for these analyses.



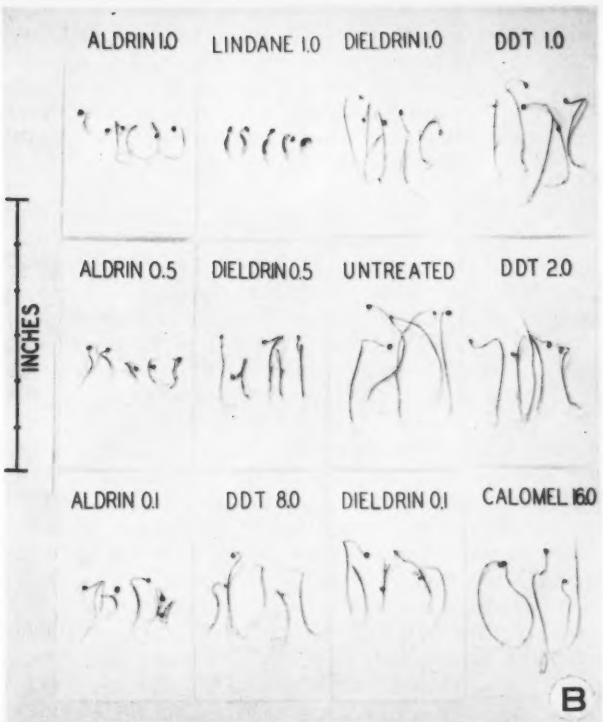


FIGURE 1. Stunting and malformation of onion seedlings caused by seed treatments with aldrin and lindane.

A. Seedlings grown under field conditions: (*Right*) Seedlings grown from untreated seeds; (*Left*) Seedlings grown from seeds treated with lindane at 1 oz. per pound of seed.

B. Seedlings grown under controlled conditions, 75° F. and 70 per cent R.H., from seed treated with various insecticides.

degrees to become a straight leaf. By this stage the small bulbs had become noticeably enlarged, the tissue was spongy and visibly deficient in water, the necks of the bulbs were about twice the size of normal plants and the leaves were stunted. The root system was limited to the initial primary root, root hairs and lateral roots being absent. All were present in the untreated plants (Figure 1, A). Chlorosis first appeared in the upper half of the leaf. Those plants that did not outgrow these conditions soon wilted and died.

Germination tests in the laboratory showed that, even at optimum moisture and temperature, seedlings from seeds treated with aldrin and lindane (Figure 1, B) were stunted and malformed. The numbers of seedlings from treated seed were not significantly different from those in the check under these conditions.

All treatments at both sites significantly reduced the amount of damage caused by the onion maggot (Table 2). In both years, seed treatments with aldrin, except at 0.1 oz., or dieldrin was significantly more effective than with calomel.

Differences in yield of marketable onions between treated and untreated plots were masked somewhat by the normal practice of thinning. This was more evident in 1953 than in 1952. Germination and growth were exceptional in 1953, as indicated by both the number of seedlings (Table 1) and the yield of marketable onions (Table 3). In 1952 all treatments except DDT at 8 oz. per pound of seed and the calomel treatment gave significantly greater yields than the check. In 1953 dieldrin at 0.5 oz. per pound of seed gave significantly greater yield than aldrin, DDT, or lindane at 1 oz. The very low yield for the lindane seed treatment was a direct result of the extreme phytotoxicity.

DISCUSSION

Seedling Emergence and Phytotoxicity

The phytotoxic effects of lindane and aldrin wettable powders were comparable to those reported by Finlayson (3) on onion seedlings grown from seed treated with 50 per cent wettable BHC. McLeod (8) and Shirk and Douglass* found that necrosis developed after BHC was applied as a wettable powder either to seed or to the furrow in which the seed was planted.

Although Hocking (6) stated that lindane does not appear to hamper germination of cereals to any noticeable degree, the results of the present investigation showed that under field conditions a commercial preparation of lindane reduced the number of onion seedlings significantly. At optimum temperature and moisture in the laboratory, germination was not affected. Hocking further concluded that the deformation was not due to the active principle, the gamma isomer. In view of the extreme malformation of onion seedlings grown from seed treated with lindane wettable powder (Figure 1, A and B), although impurities might be present, this insecticide should be regarded as a possible inhibitor of plant growth.

*Shirk, F. H., and J. R. Douglass. U.S. Dept. Agr., Twin Falls, Idaho. *Personal communication.*

TABLE 2.—TOXICANT PER POUND OF SEED AND AVERAGE PERCENTAGE DAMAGE TO ONION SEEDLINGS IN TREATMENTS AGAINST THE ONION MAGGOT AT KELOWNA, B.C., 1952, AND VERNON, B.C., 1953

Kelowna				Vernon			
Treatment	Toxicant oz./lb. of seed	Percentage damage	Arc sine transformation	Treatment	Toxicant oz./lb. of seed	Percentage damage	Arc sine transformation
Dieldrin, 50%	1.0	0.35	2.97	Aldrin, 25%	1.0	0.00	0.00
Aldrin, 50%	1.0	0.61	3.74	Dieldrin, 50%	0.5	0.00	0.00
Dieldrin, 50%	0.5	1.61	4.73	Dieldrin, 50%	1.0	0.00	0.00
Dieldrin, 50%	0.1	1.25	5.55	Aldrin, 25%	0.5	0.03	0.45
Lindane, 25%	48.0	1.59	6.40	Dieldrin, 50%	0.1	0.03	0.45
DDT, 50%	8.0	2.78	8.88	Lindane, 25%	1.0	0.03	0.50
DDT, 50%	2.0	3.85	11.06	Aldrin, 25%	0.1	0.14	1.79
Calomel	16.0	7.94	16.11	DDT, 50%	8.0	0.49	3.28
Check	—	26.77	30.61	Lindane, 25%	48.0	1.81	7.69
				Calomel	16.0	2.39	7.72
				DDT, 50%	1.0	3.51	10.10
				DDT, 50%	2.0	5.20	12.77
				Check 1	—	32.44	33.98
				Check 2	—	33.89	35.40

TABLE 3.—TOXICANT PER POUND OF SEED AND AVERAGE YIELDS OF ONIONS PER PLOT IN TREATMENTS AGAINST THE ONION MAGGOT AT KELOWNA, B.C., 1952, AND VERNON, B.C., 1953

Kelowna			Vernon		
Treatment	Toxicant oz./lb. of seed	Yield lb.	Treatment	Toxicant oz./lb. of seed	Yield lb.
Check	—	28	Lindane, 25%	1.0	9.5
Calomel	16.0	33	Check 1	—	78.5
DDT, 50%	8.0	33	DDT, 50%	1.0	81.2
Aldrin, 50%	1.0	37	Aldrin, 25%	1.0	81.4
Dieldrin, 50%	1.0	38	DDT, 50%	8.0	84.1
Dieldrin, 50%	0.1	40	Aldrin, 25%	0.5	85.2
DDT, 50%	2.0	43	Check 2	—	85.6
Lindane, 25%	48.0	43	DDT, 50%	2.0	87.0
Dieldrin, 50%	0.5	45	Dieldrin, 50%	0.1	87.1
			Aldrin, 25%	0.1	95.2
			Lindane, 25%	48.0	96.5
			Dieldrin, 50%	1.0	97.8
			Calomel	16.0	98.8
			Dieldrin, 50%	0.5	102.1

In view of the work by Scholes (10) and Walz*, the phytotoxic effects of aldrin in 1953 cannot be explained solely by impurities. Scholes reported that germination and growth rate of onion were unaffected by germination in contact with aldrin, dieldrin, isodrin, endrin, or DDT in concentrations in excess of those recommended for field work. Further, though aldrin, recrystallized aldrin, and dieldrin had no effect on the dividing cell, they had a toxic effect on the nucleus of the resting cell. Walz showed that 1 lb. of lindane per acre or 2 lb. of aldrin or isodrin applied to the furrow with onion seed did not hamper germination but altered cellular development of the seedling roots, lindane especially causing extreme polyploidy. Further, he found that most of the plants eventually died as a direct result of treatment with lindane and that recovery was slow in plants that survived the treatment of either aldrin or isodrin.

Maggot Damage

The superiority of the chlorinated hydrocarbons over calomel as a seed treatment shown by Finlayson and Handford (4) was demonstrated

*Walz, A. J. Branch Expt. Sta., Univ. Idaho, Parma, Idaho. *Personal communication.*

again in this investigation. This finding is in accord with Dustan (2), who discussed the inadequacy of calomel in severe infestations. Both Peterson and Noetzel (9) and Tozloski (11) found that seed treatments with chlorinated hydrocarbons gave economic control of the onion maggot.

Although this experiment proved only that the dieldrin seed treatment could withstand maggot attacks that caused some 30 per cent damage in the checks, further work by the author in 1954 showed that it allowed only 2.3 per cent damage in a field where 91.2 per cent of the check plants were destroyed. In view of the results, there is little doubt that dieldrin is much superior to calomel. If one considers the cost of application, then dieldrin must be given more attention. One pound of calomel costs $6.15 and treats one pound of seed, while one ounce of 50 per cent wettable dieldrin costs 30 cents and treats an equal amount of seed. Moreover, the smaller quantity of dieldrin interferes less with seeding operations.

Since DDT was previously recommended as a seed treatment it should be evaluated similarly. The degree of protection given by DDT, at one lb. of 50 per cent wettable powder per pound of seed, compares favourably with that from dieldrin at one oz. of 50 per cent wettable powder per pound of seed. DDT, at $1.50 per pound of wettable powder, cost five times as much as dieldrin to treat onion seed for any unit area. The difficulty experienced in seeding DDT-treated seed, plus the increased cost of using DDT at the rate specified, strengthens the position of dieldrin.

ACKNOWLEDGEMENTS

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FURTHER OBSERVATIONS OF FLAT LIMB OF GRAVENSTEIN[1]

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ABSTRACT

The flat-limb disease of Gravenstein apple is shown to be of virus origin. French Crab root stock was found to be a more susceptible host parent than the slower growing Anis and Antonovka stocks. Stem-grafted, apparently healthy Gravenstein trees were more susceptible to flat limb after the introduction of scions from affected trees than either root-grafted or budded trees.

INTRODUCTION

The flat-limb condition frequently appearing on apple trees of the variety Gravenstein has been described and illustrated in a previous paper (1). The evidence relative to the cause of the disease was not conclusive at that time and it seemed advisable to make further studies on the influence of the stock-scion relationship in the production of symptoms of the disease.

MATERIALS AND METHODS

Two-year-old trees of Red Gravenstein, top-worked on French Crab, Anis and Antonovka seedling stocks, were used in the experiment. Red Gravenstein scions had been worked on each of the three rootstocks by three different methods: stem grafting, root grafting and budding. Approximately 20 trees obtained by each method of propagating the rootstocks were planted in 10 ft. × 10 ft. spacing. At the time of planting no evidence of flat limb was visible on any tree.

The following year, three trees from each of the nine groups of root stocks were top-worked on the intermediate Gravenstein wood with scions from the following sources:

Wash.—Washington strain of Red Gravenstein showing severe flat limb.

Banks—Banks strain of Red Gravenstein showing moderate flat limb.

Wag.—Wagener showing a mild form of flat limb.

Forty-four trees were left as controls. A total of 81 trees were grafted with flat-limb material. Many scions failed to survive the first year and a few trees were lost from girdling by mice. The grafts on 44 trees made satisfactory growth throughout the course of the experiment.

The first symptoms of flat limb appeared on the intermediate wood the fifth year, but the majority of the trees did not show symptoms until after seven or eight years. Final observations on the presence of flat limb were made after the tenth year and prior to the removal of the trees because of crowding.

[1]Contribution No. 1568 from Botany and Plant Pathology Division, Science Service, Canada Department of Agriculture, Ottawa, Ont.
[2]Plant Pathologist, Kentville, N.S.

OBSERVATIONS

Examinations were made for the presence of flat-limb cankers on any part of the tree. The 37 trees on which the grafting was unsuccessful failed to develop symptoms of flat limb. The 44 trees on which the grafting was successful are accounted for in Table 1.

TABLE 1.—PREVALENCE OF FLAT LIMB ON TREATED TREES

Treatment of original tree	Wash.		Banks		Wag.		Total	
	Free	Affected	Free	Affected	Free	Affected	Free	Affected
Stem-grafted	0	7	1	3	1	4	2	14
Root-grafted	4	1	3	2	5	1	12	4
Budded	5	0	0	0	7	0	12	0
Total	9	8	4	5	13	5	26	18

One of the interesting results shown in Table 1 is the number of stem-grafted trees which produced flat limb as compared to the number of root-grafted or budded trees that developed the disease. The vertical totals in Table 1 indicate that the Washington and Banks strains of Gravenstein carried a more virulent virus than the variety Wagener. In addition to the results shown in Table 1, the test also showed that three of the four root-grafted trees which produced flat limb were on French Crab; the fourth was on Anis.

The relationship between the variety of root stock and flat limb is shown in Table 2. Forty of the control trees remained free from flat limb throughout the period of observation, whereas the four control trees that developed flat limb did so comparatively early and apparently had the disease when planted.

Of the trees that developed flat limb, cankers appeared on some within five years and on all of the trees within eight years after grafting. The disease did not appear on any additional trees during the last two years of the experiment. The cankers were confined to the intermediate Red Gravenstein wood. This observation indicated that the causative agent

TABLE 2.—FLAT LIMB AND THE VARIETY OF ROOTSTOCK

Rootstock	Control		Grafted flat limb	
	Free	Affected	Free	Affected
French Crab	16	0	4	9
Anis	13	2	11	4
Antonovka	11	2	11	5
Total	40	4	26	18

of the disease travelled from the scions into the intermediate wood of the trees and there caused the development of cankers.

The evidence that the symptoms are more prevalent on stem-grafted trees than on those propagated by root grafting is in agreement with early work by McAlpine (2) in Australia. This same evidence is readily obtained from observations in commercial orchards and nurseries where the variety Gravenstein has been propagated. Nurserymen have found that there is little if any flat limb found in budded trees of the variety Gravenstein. When young trees in an orchard are frame-worked or grafted to Gravenstein the disease will appear more frequently. These observations imply that the stem portions of the stock may affect symptom production.

DISCUSSION

Studying a disease of this nature, which requires from four to eight years to produce indisputable symptoms, is less satisfying than many pathological problems. However, the work to date has yielded some interesting observations that might be valuable in the planning of any future work on the problem.

The data presented in this paper confirm the virus origin of the disease since the scions from affected trees grafted to apparently healthy trees stimulated the production of flat-limb symptoms. Trees on which the grafting was unsuccessful continued normal growth. Of the three sources of disease the Washington and Banks mutants of Gravenstein carried more virulent flat-limb virus than did Wagener.

The experimental results show that Gravenstein is more susceptible to flat limb when growing on French Crab than when on either Anis or Antonovka stock. When comparisons are made between the methods of propagation it is evident that those trees which were stem-grafted to Gravenstein were more susceptible to the disease than those which had been budded or root-grafted. The 2- and 3-year delay in symptom expression suggests that, under some conditions, the virus may be latent.

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SOME FACTORS AFFECTING HULL ADHERENCE IN BARLEY[1]

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ABSTRACT

The effects of stage of maturity, and methods of drying after cutting, on hull adherence were evaluated on different varieties of barley by determining their susceptibility to hull damage when exposed to rough handling, and by observing the percentage of abnormally projecting acrospires in subsequent germination.

The percentage of kernels with hull damage and with abnormal acrospire growth in subsequent germination in the three varieties tested were highest when they were harvested late, i.e., when ready for combining; and lowest when harvested early, i.e., the mid-dough stage.

The three barley varieties, G.B. 19, Montcalm and O.A.C. 21, when dried in the field in uncovered stooks had a significantly higher percentage of both damaged kernels and abnormal acrospire growth than when dried in the barn or in the field covered by canvas or capped with sheaves.

Significant differences in susceptibility to damage and abnormal acrospire growth associated with differences in locations and varieties were found when 25 barley varieties were grown in six counties of Ontario in 1952 and 1953. In these tests a highly significant positive correlation was found to exist between hull damage and abnormal acrospire growth. However, some notable exceptions occurred, suggesting that the seed coat as well as the hull of the barley kernel is an important factor in obtaining normal acrospire growth during germination.

A relatively simple method of evaluating hull adherence in barley varieties is described.

INTRODUCTION

Malting barley production is an important part of the agricultural economy of Canada, since approximately 30 per cent of barley produced is used for malting purposes. Therefore malting quality is of utmost importance in varieties intended for the malting industry.

In addition to extractable barley constituents and other chemical properties, there are also a number of physical properties which must be taken into account in assessing malting quality. The barley kernels should be of medium size, short and plump, and have a tough, closely attached hull, which should remain intact throughout the whole malting process. This requires the barley breeder to evaluate the hull adherence of strains in the breeding program.

During normal germination of the barley grain the acrospire or shoot does not break through the investing lemma but forces its way upwards beneath it and appears first at the apex of the grain (8). Damaged or loose hulls may expose the acrospire during the germination period. Projecting acrospires are likely to be damaged or broken by the stirring machinery in the malting process, thus retarding or stopping growth. As a result the desired chemical changes in the endosperm do not take place, and a ragged, unsatisfactory malt will be produced.

[1] Condensation of thesis submitted to the Graduate School, University of Toronto, by E. Reinbergs, in partial fulfilment of the requirements for the degree of Master of Science in Agriculture.

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The results of numerous investigations (4, 6, 11, 12) indicate that the main cause of mechanical damage in barley is faulty machine adjustment and operation during threshing. However, it has been reported by several authors that the moisture content in the threshed grain (11, 12), the variety (6, 9, 11), and the location (6, 7, 9) all may change the susceptibility to damage of the barley kernel.

Malloch (11), using a special apparatus for damaging barley experimentally, showed that rough handling increases the susceptibility to subsequent damage. He found also that susceptibility to damage may be increased if the barley grain is subjected to repeated wetting and drying. This indicates that the length of time the grain has been in the stook may be a factor of considerable significance.

Several authors (6, 10, 13) have discussed the percentage of hull of different barley varieties and its role in malting quality. In general thick hulls adhere less firmly than thin ones (1, 6).

The purpose of this paper is to report on investigations with respect to the influence of drying methods and the stage of maturity at harvest time on the hull adherence in barley, the differences in varietal susceptibility to damage at different locations, and the influence of hull damage on the acrospire growth habit in the barley kernel during germination.

MATERIALS AND PROCEDURE

The experimental work on different drying methods and harvesting at different stages of maturity was conducted at the Ontario Agricultural College in 1952 and 1953.

In 1952, two varieties of barley, G.B. 19 and Montcalm, were tested and in 1953 O.A.C. 21 also was included in the test. Montcalm is the variety most widely grown for malting purposes in Canada, while O.A.C. 21 is the standard for malting quality. G.B. 19 was a promising variety of barley that had been selected at the Ontario Agricultural College from the cross Stephan x Galore.

The barley varieties were grown in half-acre blocks except Montcalm in 1952, when only 1/100 of an acre of this variety was available. When the barley grain had reached the soft dough stage a split-plot design, for the different drying methods and stages of maturity, was outlined in the most evenly matured place in each block of the three barley varieties. The stages of maturity were used as the main plots, the drying methods as subplots. For Montcalm in 1952 only different stages of maturity were used. The experiment was replicated three times. The size of the subplots was 48 square feet.

Three different stages of maturity were used, viz., *early*—when the grain was in mid-dough stage; *medium*—when the grain was in late-dough stage and ready to cut with the binder; *late*—when the grain was flinty and ripe enough for combining. Approximately seven days occurred between stages of maturity. For the variety O.A.C. 21 only two stages of maturity, *medium* and *late*, were used.

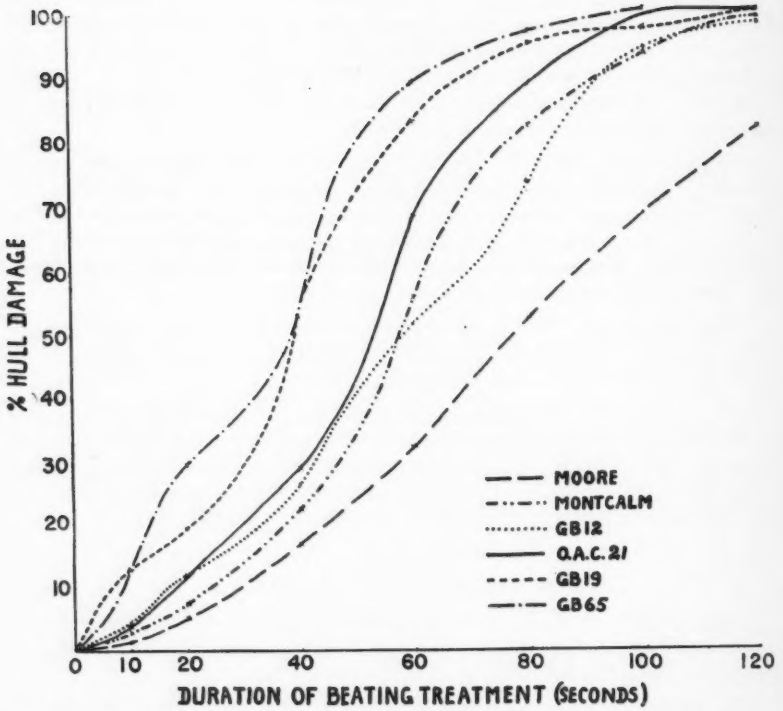

FIGURE 1. Per cent hull damage of six barley varieties grown in Peel County, Ontario, in 1953, as affected by length of time in modified pearler.

For each stage of maturity four different drying methods were employed: hanging in the barn; stooking in the field and covering with canvas; stooking in the field and capping with sheaves; and stooking in the field and leaving uncovered. The sheaves dried in the barn were taken in immediately after cutting. The sheaves dried outside were left in the stooks for two weeks, when they were taken into the barn and stored, together with the barn-dried ones, until threshing.

To determine the differences in varietal susceptibility to damage in different locations in Ontario, 25 varieties of barley from the Ontario Agricultural College regional tests were investigated in 1952 and 1953. The tests were conducted in six different countries of Ontario: Brant, Middlesex, Peel, Simcoe, Waterloo, and Wellington.

Before testing, all the grain was brought to a uniform moisture content, ranging from 9 to 10 per cent as measured by Steinlite moisture tester, and the small kernels were removed by means of a screen with slots 2.2 mm. wide and 13 mm. long.

The hull adherence in the barley varieties was tested by determining their susceptibility to damage. These determinations were carried out by

means of a reconstructed Strong-Scott experimental pearler. The principle of this machine is based on a revolving abrasive stone surrounded by stationary mesh wire. To subject the barley kernels to damage caused by beating instead of grinding, the stone of the pearler was replaced by a ridged plywood disk with four tin wings on each side. The mesh wire was replaced by a smooth strip of tin. The speed of the pearler was adjusted to 1400 r.p.m. Triplicate samples, consisting of 400 undamaged kernels, were put through the modified pearler.

From each of the treated samples 100 kernels were picked at random and the percentage of kernels with hull damage was determined. A barley kernel was considered damaged when at least one-third of the hull was removed, or the germ was exposed. The cracked or broken kernels were not included in the determinations.

In a preliminary test of the method in 1952, the duration of the beating treatment influenced the differences in per cent damage of different barley varieties. This test was repeated in 1953, using six barley varieties which differed greatly in hull adherence. The results of this test are shown in Figure 1. It can be seen from Figure 1 that, where the number of damaged kernels approaches zero or 100 per cent, the differences among five of the six varieties decrease considerably. This indicates that the barley varieties have to be exposed to a certain amount of rough handling before differences in hull adherence will show up.

The barley at plant breeding stations during harvesting, threshing, and cleaning is handled with the greatest possible care, and therefore is less exposed to damage than the barley harvested by commercial machines. Therefore, it would seem to be necessary for a plant breeder to expose the barley varieties to a certain amount of rough handling before attempting to predict their behaviour under normal production conditions.

An attempt was made to adjust the time of treatment for the various tests in such a manner that the number of damaged kernels would fall in the 20 to 80 per cent range. This resulted in many separate statistical analyses in this study. The duration of the beating treatments ranged from 20 to 60 seconds.

In addition to the determination of the percentage of damaged kernels, the percentage of kernels giving an abnormal acrospire growth in subsequent germination after beating was determined in 25 varieties from the regional tests in 1952 and 1953, and in the tests of stages of maturity and drying methods in 1953. For this purpose the same 100 barley kernels which were used for the damage determinations were germinated in Petri dishes on pads of filter paper at 58 to 60° F. The kernels with abnormal acrospire growth were counted after a 72-hour germination period. By this time the acrospires of the undamaged kernels growing under the lemma had reached the apical end of the kernels. Acrospires emerging at the side or at the basal end of the kernels during the germination period were considered as growing abnormally. All the results, obtained on a per cent basis, were transformed into the form $p = \sin^2\theta$ for analyses of variance. The transformed data only are presented.

TABLE 1.—PER CENT HULL DAMAGE AND ABNORMAL ACROSPIRE GROWTH OF G.B. 19, MONTCALM AND O.A.C. 21 BARLEY, HARVESTED AT THREE DIFFERENT STAGES OF MATURITY (MEANS OF TRANSFORMED DATA)

Stages of maturity	1952		1953		
	G.B. 19	Montcalm	G.B. 19	Montcalm	O.A.C. 21
			Damage		
Mid-dough	21.6	15.4	30.7	34.8	——
Late-dough	33.8	22.9	36.1	42.4	48.4
Ripe	39.6	28.4	44.3	47.7	53.6
L.S.D.—0.05	8.1	2.4	3.1	2.1	0.9
—0.01	13.4	3.2	5.1	3.4	2.1
			Abnormal acrospire growth		
Mid-dough	——	——	27.5	32.8	——
Late-dough	——	——	29.3	34.2	37.5
Ripe	——	——	39.3	38.9	47.8
L.S.D.—0.05	——	——	2.9	2.0	1.1
—0.01	——	——	4.7	3.3	2.6

TABLE 2.—PER CENT HULL DAMAGE AND ABNORMAL ACROSPIRE GROWTH OF G.B. 19, MONTCALM AND O.A.C. 21 BARLEY, DRIED BY FOUR DIFFERENT METHODS (MEANS OF TRANSFORMED DATA)

Drying methods	1952	1953		
	G.B. 19	G.B. 19	Montcalm	O.A.C. 21
		Damage		
In barn	28.1	36.9	38.8	49.8
In field under canvas	30.8	35.0	41.0	48.6
" " capped	31.8	36.0	40.2	50.0
" " uncovered	36.0	40.2	46.5	55.6
L.S.D.—0.05	1.5	1.2	1.2	1.3
—0.01	2.0	1.6	1.6	1.7
		Abnormal acrospire growth		
In barn	——	29.6	31.3	37.1
In field under canvas	——	31.3	34.9	42.1
" " capped	——	31.7	35.6	42.6
" " uncovered	——	35.5	39.4	48.7
L.S.D.—0.05	——	0.9	1.0	1.2
—0.01	——	1.2	1.3	1.6

RESULTS AND DISCUSSION

Effects of Stages of Maturity

The data in Table 1 indicate that harvesting at different stages of maturity influenced the susceptibility to damage and the subsequent abnormal acrospire growth of G.B. 19, Montcalm and O.A.C. 21 barley varieties to a considerable extent.

The per cent damage was the highest in all three of the barley varieties tested when they were harvested late, i.e., when ready for combining. In G.B. 19 and Montcalm the per cent damage was significantly lower when the varieties were harvested early, i.e. in the mid-dough stage. Harvesting in the late-dough stage gave intermediate results in these varieties.

The per cent abnormal acrospire growth in 1953 in all three of the varieties tested had the same trend as the per cent damage.

Also the different drying methods influenced considerably the per cent of damaged kernels in the three barley varieties (Table 2). The barley varieties when dried uncovered in the field gave a significantly higher percentage of damaged kernels than when dried in the barn or covered in the field. Covering with a canvas and capping gave varying results as compared with barn drying. It is possible that the canvases or sheaves did not protect all the stooks from the dew and rain to the same degree.

The per cent abnormal acrospire growth, as was the case in harvesting at different stages of maturity, followed the trend of the per cent damage.

The combined effects of the stages of maturity and drying methods upon the per cent damage and abnormal acrospire growth of the three barley varieties tested in 1953 can be seen in Figure 2.

The three varieties tested were not influenced to the same degree by the different stages of maturity and drying methods. In G.B. 19 barley the per cent damage in early and medium stages of maturity at all drying methods was lower than in the late stage of maturity. Montcalm, however, at the early stage of maturity when it was dried uncovered had a greater per cent damage than at the medium stage of maturity, when dried covered. It was almost the same as at the late stage of maturity when capped or dried in the barn. O.A.C. 21 barley cut at the late stage of maturity, dried in the field covered, or dried in the barn, gave similar results to those obtained when cut at the medium stage of maturity and dried uncovered.

These results suggest that exposure of the barley to changing climatic conditions during the drying time in some cases may influence the hull adherence as much as different times of cutting.

The general trend, however, was the same in the three strains. The lowest susceptibility to damage was obtained by early cutting and covering the stooks, or by drying in the barn; the highest by late cutting and drying the sheaves in the field uncovered.

Malloch (11) found that the susceptibility to hull damage of the barley grain could be increased under laboratory conditions by wetting and drying the grain. He suggested that capping of barley stooks would probably reduce the threshing damage. This is in agreement with the results

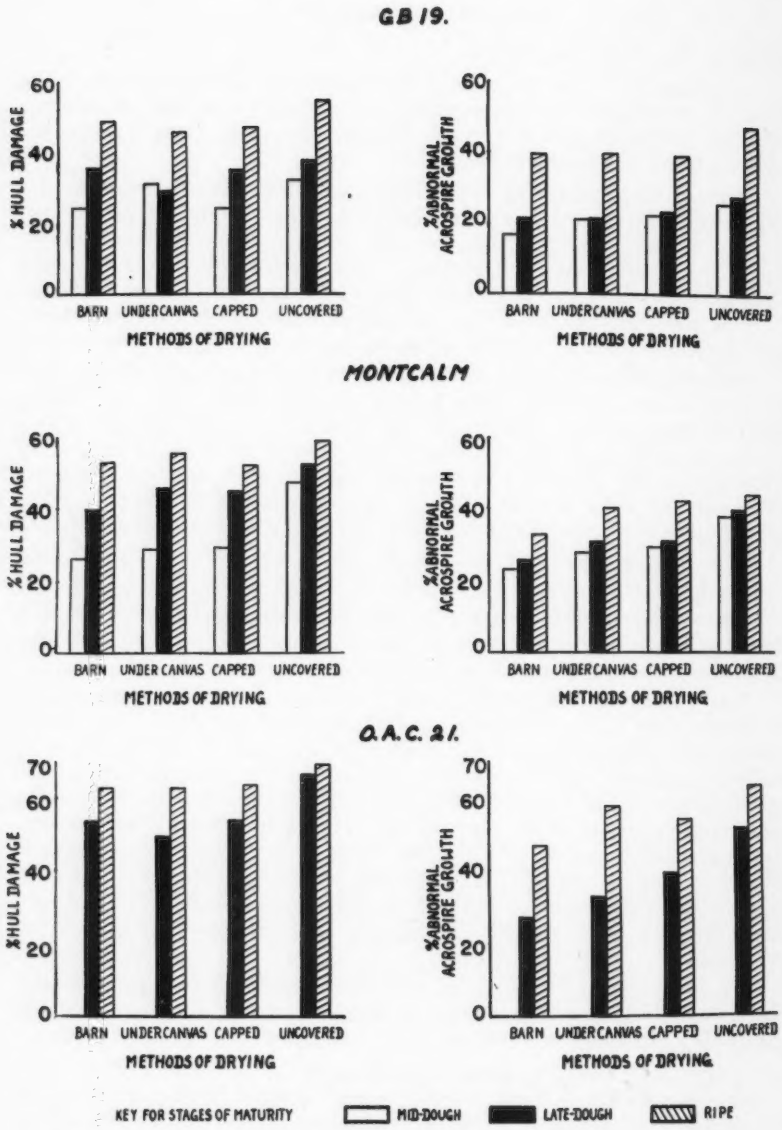

FIGURE 2. Per cent hull damage and abnormal acrospire growth of G.B. 19, Montcalm and O.A.C. 21 barley, cut at different stages of maturity and dried by four different methods in 1953. (Means of transformed data).

obtained in this investigation. As the floral glumes of a barley kernel are very good capillary conductors (3), it seems very probable that not only rain but also heavy dew may have the same effect as alternate wetting and drying under laboratory conditions.

The changing climatic conditions seem to influence not only the hull adherence but also the properties of the hull itself. In many cases during the experiment the hulls of the damaged kernels were not peeled, but rather broken off in small pieces.

It has been found (1) that cutting at different stages of maturity may influence the wrinkling of the barley hulls, and that the moisture content (4, 11) and ash content (2, 5) may change the brittleness of the barley awns and hulls. This indicates that several factors affecting the hull properties during the maturing process and drying time are responsible for the differences in susceptibility to damage in barley.

The information obtained with respect to the influence of stages of maturity and drying methods on hull adherence does not offer much in the way of practical possibilities of reducing the per cent of damaged kernels, because the malt-houses are interested in completely mature grain only, and combining is becoming the most popular method of harvesting barley.

TABLE 3.—PER CENT HULL DAMAGE AND ABNORMAL ACROSPIRE GROWTH OF BARLEY GROWN AT SIX LOCATIONS IN ONTARIO IN 1952 AND 1953 (MEANS OF 25 VARIETIES)

Location	1952	1953
	Damage	
Wellington	25.4	49.1
Waterloo	30.3	35.6
Simcoe	36.2	47.4
Brant	36.3	42.2
Peel	36.7	22.9
Middlesex	38.7	39.7
L.S.D.—0.05	1.5	1.5
—0.01	2.0	1.9
	Abnormal acrospire growth	
Wellington	27.0	39.9
Waterloo	29.9	32.3
Simcoe	36.4	43.2
Brant	35.6	40.3
Peel	36.3	21.9
Middlesex	40.2	36.8
L.S.D.—0.05	1.4	1.4
—0.01	1.8	1.9

TABLE 4.—PER CENT HULL DAMAGE AND ABNORMAL ACROSPIRE GROWTH OF 25 BARLEY VARIETIES GROWN IN ONTARIO IN 1952 AND 1953

(MEANS FOR SIX LOCATIONS)

1952			1953		
Variety	Damage	Abnormal acrospire growth	Variety	Damage	Abnormal acrospire growth
Moore	22.2	25.2	Moore	25.3	23.7
G.B. 69	27.2	22.2	G.B. 69	30.0	25.3
G.B. 13	27.5	25.7	G.B. 66	33.7	31.0
G.B. 58	28.3	36.1	G.B. 59	34.8	35.8
G.B. 71	29.7	25.2	Montcalm	35.2	33.0
G.B. 12	29.8	36.1	G.B. 71	35.6	30.3
G.B. 59	30.6	35.6	G.B. 13	36.5	29.0
G.B. 63	30.7	36.1	G.B. 58	37.3	37.7
G.B. 60	31.5	35.8	G.B. 21	37.4	37.7
G.B. 21	32.5	38.3	G.B. 60	37.4	36.9
G.B. 61	33.2	37.3	G.B. 63	37.5	37.4
G.B. 66	33.6	32.1	G.B. 34–11	38.2	35.3
Galore	34.2	34.9	G.B. 37	38.3	36.5
O.A.C. 21	34.3	31.5	G.B. 61	39.2	38.5
G.B. 53	34.8	33.4	G.B. 12	40.0	33.6
3092A	35.7	33.6	G.B. 53	40.1	32.2
G.B. 34–11	35.8	36.5	O.A.C. 21	41.0	34.8
UM 1020F	36.4	32.6	Galore	42.0	37.5
Montcalm	36.7	36.6	UM 1020F	43.7	35.0
G.B. 37	38.0	36.7	G.B. 52	44.2	40.4
G.B. 72	38.1	32.5	3092A	46.0	41.0
G.B. 52	38.3	40.3	G.B. 72	46.1	39.5
G.B. 19	38.7	36.8	G.B. 64	47.0	41.7
G.B. 64	39.5	39.3	G.B. 19	48.0	45.0
G.B. 65	50.8	45.0	G.B. 65	52.1	44.8
L.S.D.—0.05	3.1	2.8		3.0	2.9
—0.01	4.0	3.7		3.9	3.8

The Effects of Locations and Strains

The data from Tables 3 and 4 indicate that the 25 varieties significantly differed in susceptibility to damage and abnormal acrospire growth, and that the location had a definite influence.

In 1952 the 25 strains grown in Middlesex County were highest in both per cent damage and in abnormal acrospire growth. Alternatively, the same strains grown in Brant County were lowest in both of these characteristics. The results were also low in Waterloo. There were no significant differences in the results obtained in Peel, Simcoe, and Brant. In 1953, however, the location effects were noticeably different. In this year the lowest per cent of both damage and abnormal acrospire growth were obtained in Peel County, and the highest in Wellington.

The means of the varieties show (Table 4) that in both years Moore barley had significantly fewer damaged kernels than the other 24 varieties tested. G.B. 69 also had a very low percentage of damaged kernels. On the other hand, G.B. 65 had the highest number of damaged kernels and was significantly more susceptible to damage than any other variety. The other varieties studied showed susceptibility to damage intermediate between these extremes.

In 1952, thirteen of the varieties were more resistant to damage than the standard malting variety O.A.C. 21. Montcalm was more susceptible

TABLE 5.—CORRELATION COEFFICIENTS FOR THE PER CENT DAMAGE AND ABNORMAL ACROSPIRE GROWTH OF 25 BARLEY VARIETIES GROWN AT SIX LOCATIONS IN ONTARIO IN 1952 AND 1953

	"r" value
Per cent damage 1952 and 1953	0.838
Per cent abnormal acrospire growth 1952 and 1953	0.830
Per cent damage and per cent abnormal acrospire growth 1952	0.721
Per cent damage and per cent abnormal acrospire growth 1953	0.871
Necessary "r"—0.05	0.396
—0.01	0.505

to damage than O.A.C. 21, but the difference was not significant. Eleven of the varieties tested were more susceptible to damage than O.A.C. 21.

Correlation coefficients (Table 5) for the mean per cent damage and per cent abnormal acrospire growth of the 25 varieties indicate that most of the varieties behaved similarly in both years. However, data from Table 4 indicate that a few varieties, including Montcalm, behaved differently in the two years in which they were tested.

The differences in hull adherence among varieties suggest some promising practical possibilities. Many of the barley varieties tested had much better hull adherence then the common malting varieties, O.A.C. 21 and Montcalm, thus indicating that new varieties with much better hull adherence can be developed.

Per Cent Damage Versus Per Cent Abnormal Acrospire Growth

Malloch (11) states that 4 per cent of damaged barley kernels may lead to the loss of 15 per cent of hulls in the malting process. No literature is known to the writers where the per cent of damaged kernels is compared with the per cent abnormal acrospire growth during the malting process of the barley.

In the present investigation, the correlation coefficients calculated for the means of per cent damaged kernels and the means of per cent abnormal acrospire growth (Table 5) indicate that in both years there was a significant positive correlation between these two characters in the 25 barley varieties tested. Figure 2, however, shows that the per cent abnormal acrospire growth was considerably lower at all the stages of maturity and drying methods used than the per cent damage of the same barley kernels. Most of the means of the varieties in the six locations in 1952 and 1953 (Table 4) showed the same tendency. However, some varieties, e.g. G.B. 59, G.B. 21, and G.B. 58, had a higher per cent abnormal acrospire growth than the per cent damage. This indicates that with the

same per cent visible damage some varieties under certain conditions may differ in per cent abnormal acrospire growth. This suggests that besides the hull, its properties and degree of removal, still other morphological structures of the barley kernel may have an effect upon the growth of the acrospire.

The growing acrospire during the germination process pushes forward not only under the hull but also under the seed coat of the barley kernel. During the germination tests some completely dehulled barley kernels were observed with the acrospire growing normally under the seed coat. On the other hand some kernels with undamaged hulls gave abnormal acrospire growth.

It has been found (14) that the seed coat is of different thickness in different barley varieties, and that the properties of the seed coat may be influenced greatly by the environment. These observations, together with the data obtained in the experiments presented in this paper, suggest that both the seed coat and the hull are important in securing a normal acrospire growth in barley.

How much each of these contributes to the normal acrospire growth in the different varieties and various environments, and how great is the role of the sticky substance that holds them together, are problems that need further investigation.

Aberg and Wiebe (1) and Harris (6) have indicated that thick hulls in general adhere less firmly to the barley kernel than thin hulls. However, the varieties used in this investigation were found to vary so little in per cent hull that no attempt was made to correlate this factor and hull adherence.

ACKNOWLEDGEMENTS

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A PORTABLE FORAGE CROP CHOPPER[1]

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ABSTRACT

A small portable forage crop chopper, constructed from the reel and cutterbar assembly of a power lawn mower, is described. The unit is powered by the engine originally used on the power lawn mower. It has been designed for chopping forage plot material required for sampling purposes. The low cost of construction, compactness, weight, and size makes it well suited and easily transported for the conducting of regional tests.

INTRODUCTION

The portable forage crop chopper described was developed to be used for test work away from centralized research institutions.

CONSTRUCTION

A 20-inch standard reel type lawn mower cutterbar assembly and engine were mounted on a wooden frame. The reel is driven at 525 r.p.m. through a jack shaft and V-belt drive, as illustrated in Figure 1. The machine is 50½ inches long, 26 inches wide and 38 inches high. The height is reduced to 29 inches for transportation by the removal of the lower sleeve section of each leg. The entire unit weighs 160 pounds. The chopped forage is caught in the drawer under the reel. The drawer is sloped at the back from 26 inches long at the top to 21 inches at the bottom, is 6½ inches wide and 8 inches deep.

OPERATION

Grab samples of the harvested forage are bulked and hand fed into the chopper. When the chopping is complete the reel is stopped, the drawer is withdrawn, and the necessary quantity of chopped forage is weighed out.

DISCUSSION

This machine has been successfully used for one year on illustration Stations in the Lennoxville, Quebec, district. As an example of its performance, 272 second-crop alfalfa hay samples have been chopped in 5½ hours.

[1]Contribution from Illustration Stations Division, Experimental Farms Service.
[2]Agricultural Research Officer, Illustration Stations Division, Lennoxville, Que.

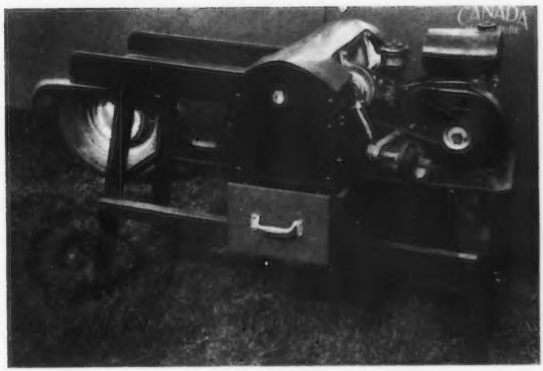

FIGURE 1. Side view of portable forage chopper.

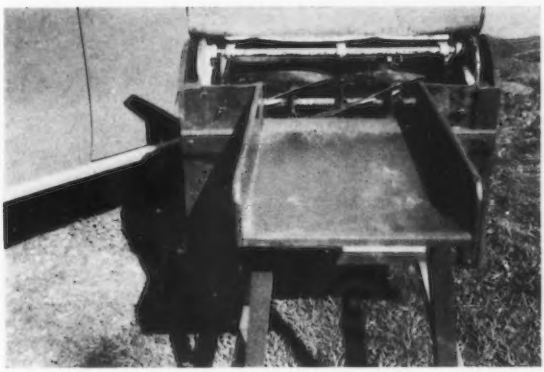

FIGURE 2. End view of chopper, showing reel cutter.

PHYSIOLOGIC SPECIALIZATION OF WHEAT STEM RUST IN CANADA, 1919 TO 1955[1]

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[Received for publication September 19, 1956]

ABSTRACT

From 1919 until shortly after 1930 the races of wheat stem rust most prevalent in Canada were: race 21, the race group 3-18-36, and the race group 17-29 which again assumed importance from 1940 to 1948. Race 49 was widely prevalent from 1927 to 1932. Race 56, first found in Canada in 1931, was the predominant race from 1934 to 1949. Race 15B, discovered shortly before 1940 and first found in Canada in 1946, was predominant from 1950 to 1955.

The influence of changes in the wheat varieties under cultivation on the rust race population is discussed and it is postulated that a north-to-south movement of rust spores late in the summer plays an important part in the perpetuation of races selectively propagated in northern areas.

Recently, biotypes of certain races have become important in relation to varieties now in cultivation and new varieties in the course of production. Methods of identification of such biotypes by means of accessory differential hosts are discussed in relation to the breeding or rust-resistant varieties.

A brief account is given of races identified from collections of aecia from barberry.

INTRODUCTION

An earlier publication (8) has recorded the physiologic races of wheat stem rust, *Puccinia graminis* Pers. f. sp. *tritici* Erikss. & Henn., found in Canada during the period 1919 to 1944. Since 1944, important changes have taken place in the physiologic-race population in Canada and other parts of North America. Because of this fact, and because of a considerable change in the last few years in the attitude of rust investigators towards these races, it seems desirable to review the physiologic-race studies performed in Canada up to the present time and to discuss the significance of the rust races in the light of present concepts.

PHYSIOLOGIC-RACE SURVEYS

The collection and identification of physiologic races is done primarily to assist the plant breeder concerned with breeding for rust resistance because it is essential that he should know about the existence of any rust strains pathogenic on the plant material he works with. Mostly, the rust collections analysed are randomly selected in areas where stem rust occurs on cereals but attempts are usually made to obtain collections from various cereals and grasses.

The determination of year-to-year trends in the distribution of the more common races presents no difficulty. It is much more difficult to detect the presence of races or biotypes that occur only in trace quantities.

[1]Contribution No. 1564 from the Botany and Plant Pathology Division, Science Service, Canada Department of Agriculture, Ottawa, Ont.

[2]Officer-in-Charge, Plant Pathology Laboratory, and Plant Pathologist, respectively.

TABLE 1.—PHYSIOLOGIC RACES OF *P. graminis* F. SP. *tritici* COLLECTED ON CEREALS AND GRASSES IN CANADA FROM 1919 TO 1936 WITH A RECORD OF THE NUMBER OF TIMES EACH RACE WAS COLLECTED EACH YEAR

Race	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	
1	2	1	—	—	—	—	—	—	—	2	11	2	2	2	—	1	—	—	23
2-23	—	—	—	—	1	—	—	—	—	4	—	—	—	—	1	—	—	—	6
3-18-36	4	11	6	14	10	16	113	211	204	154	69	94	82	26	6	29	16	10	1075
9	4	6	2	3	—	—	—	1	4	—	—	—	—	—	—	—	—	—	20
10	—	—	—	—	—	—	—	—	—	—	—	—	3	4	—	—	—	—	7
11-32	2	9	3	3	5	9	3	12	4	5	12	1	3	5	—	—	2	5	83
12	—	2	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	—	7
14	—	—	—	—	—	—	—	2	16	2	5	4	7	2	4	—	—	—	42
15	1	—	—	—	—	—	—	2	8	21	1	—	—	1	—	—	—	—	34
16	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	2
17-29	9	48	28	16	10	1	13	29	19	17	28	4	4	6	1	4	5	15	257
19	1	—	—	—	—	—	—	1	1	6	4	1	—	17	3	—	5	4	43
21	4	—	4	24	—	1	44	84	133	103	26	22	29	15	11	20	14	7	541
24	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
27	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
30	—	1	—	—	—	—	1	7	7	—	—	—	—	—	—	—	—	—	16
33	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	2
34	—	—	—	1	3	7	1	4	10	15	4	14	25	12	12	28	36	11	183
35	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
38-39	—	—	—	—	—	—	—	18	26	32	66	39	10	7	6	4	5	31	244
40	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
48	—	—	—	—	—	—	—	2	—	—	2	—	—	—	—	—	—	—	4
49	—	—	—	—	—	—	—	3	8	14	68	8	17	17	4	5	—	5	149
50	—	—	—	—	—	—	—	—	4	—	6	—	4	1	2	—	—	—	17
51	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
52	—	—	—	—	—	—	—	1	3	6	—	—	1	—	—	—	—	—	11
53	—	—	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	2
56-125	—	—	—	—	—	—	—	—	—	—	—	—	4	10	3	55	89	153	314
63	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
64	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
74	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
75	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
77	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
78	—	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	4
81	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1
83	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
84	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
86	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
87	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
89	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
97	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
113	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	2
123	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1
	28	78	44	61	29	39	175	378	450	391	306	192	195	129	53	146	172	241	3107

								378	450	391	306	192	195	129	53	146	172	241	3107

TABLE 2.—PHYSIOLOGIC RACES OF *P. graminis* F. SP. *tritici* COLLECTED ON CEREALS AND GRASSES IN CANADA FROM 1937 TO 1955 WITH A RECORD OF THE NUMBER OF TIMES EACH RACE WAS COLLECTED EACH YEAR

Race	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	
1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	—	—	—	1	4
2-23-59	—	—	1	—	—	2	2	—	—	—	1	—	—	2	2	4	6	6	—	26
3-18-36	12	8	1	8	11	4	—	—	—	5	—	1	2	—	—	—	—	—	—	52
9	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	2
10	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1	—	3
11-32-179	—	10	3	3	1	—	—	—	2	—	3	—	1	—	1	1	1	1	19	46
14	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
15	1	2	1	1	1	1	—	—	—	3	4	1	—	82	85	271	253	285	202	1193
16	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	2
17-29-37	13	9	4	51	90	19	26	17	17	29	5	37	10	5	5	—	7	31	20	395
19	17	21	5	5	8	12	2	13	3	8	—	1	1	1	—	—	1	—	—	98
21	4	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	6
30	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
34	4	5	—	3	—	1	—	—	—	—	—	—	—	—	—	1	—	—	2	16
38-39	17	26	18	12	5	11	10	16	4	25	9	35	13	1	5	2	2	5	1	217
48	—	—	—	—	1	—	—	—	—	1	—	—	1	—	3	2	1	14	16	39
49	4	3	—	—	1	—	—	—	3	2	—	—	—	—	1	—	1	—	—	15
50	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
56-125	106	202	117	150	90	47	66	100	50	72	98	56	69	53	71	25	28	15	43	1458
61	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
63	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
69	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	2
73	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
74	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
78	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
80	—	—	—	—	1	—	—	—	1	—	—	1	1	—	—	—	—	—	—	4
87	—	—	1	—	—	—	—	—	1	—	1	—	—	—	—	—	—	2	1	6
92	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
96	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
98	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	2
102	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
113	1	—	—	—	—	—	4	—	—	—	—	—	—	1	—	—	1	—	—	7
118	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
136	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
139	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	4	1	1	8
140	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
147	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
152	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
177	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
183	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
192	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
231	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1
	183	291	156	234	215	99	111	147	83	145	123	132	100	147	178	307	307	361	306	3625

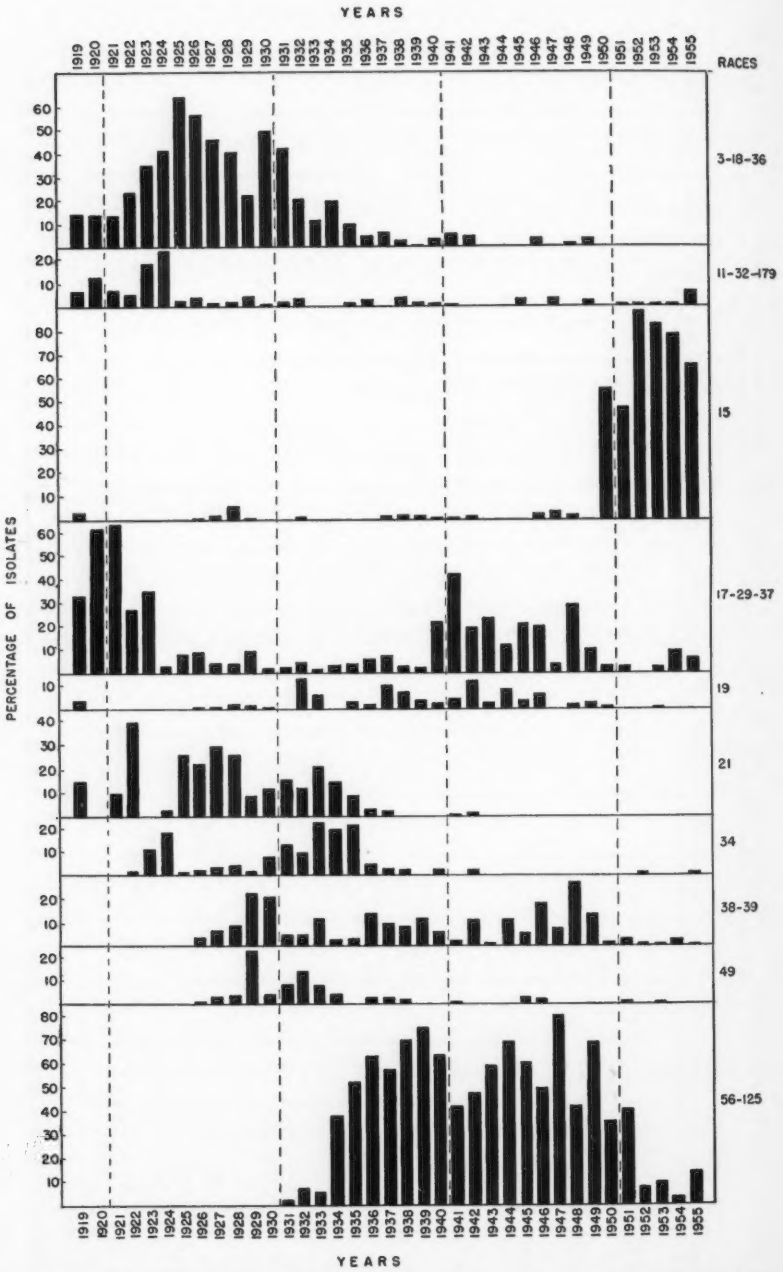

FIGURE 1. Diagrammatic representation of the prevalence, in Canada, of 10 physiologic races or race groups of wheat stem rust during the period 1919-1955.

It has long been realized that the number of randomly selected rust collections studied—in Canada usually of the order of two or three hundred—is inadequate for this purpose. It is for this reason, chiefly, that the study of random rust collections is supplemented by the use of "rust nurseries" designed to detect rarely-occurring strains of rust. In any given period the nurseries contain those varieties that serve as sources of resistance in plant breeding programs or include other varieties that are thought to show promise for this purpose.

Rust surveys have been carried out in Canada annually since 1919 and, except in certain years prior to 1925 and during the period 1930-1935, the surveys have included rust collections from rust nursery plots grown in many parts of the country.

The race surveys, though inadequate for the detection of rarely occurring races, provide a satisfactory record, for the period 1919-1955, of the prevalence of races of any appreciable importance in Canada. The frequency of collection of wheat stem rust races is recorded in Tables 1 and 2 and is summarized graphically, for the more important races, in Figure 1.

Some of the facts concerning race distribution are worth mentioning. When the surveys were commenced, the races of most significance in the Prairie Provinces were the following: Race 17, together with the related race 29 which, under some environmental conditions, cannot be readily distinguished from it; race 21; and the race-group composed of the related races 3, 18, and 36. These, together with the rather less common races 9 and 11, composed the bulk of the stem rust isolates for the first few years of the surveys. It may be noted here that all these races were virulent to the then widely grown wheat variety Marquis. Races 17 and 29 were widely prevalent from 1919 to 1929, and again from 1940 to 1948, but were less frequently found in the intervening years 1930-1939. Race 21 was important from 1919 to 1935 but was thereafter collected infrequently and has not been found since 1942. The race group 3-18-36 was very important from 1919 to 1931 but diminished thereafter to become of virtually no significance after 1941. Race 38, which has occurred annually from 1926 to 1955, was most prevalent in Eastern Canada. Its relative scarcity in the Prairie Provinces was probably due to the fact that Marquis and most other varieties of spring wheat grown there were somewhat resistant to it. Of other races present in the earlier survey years, race 49 had considerable prevalence from 1927 to 1932. Since then it has been found only occasionally and in small amounts. Race 34 was present annually from 1922 to 1938 but was never important except possibly in the period 1933-1935. It has been found only three times since 1942.

One of the most important changes in the race population during the period of the surveys was the establishment of race 56 as the predominant wheat stem rust race in North America in the early thirties. This race, first collected in the United States in 1928 (10, 13) and in Canada in 1931, had become the predominant race by 1934 and remained so until it was displaced from this position by race 15B in 1950. It is likely that the widespread cultivation in the early thirties of the wheat variety Ceres,

which is particularly susceptible to race 56, was a factor favouring the establishment and increase of this race (3, 13, 15).

Another important race change occurred in 1950 when race 15B suddenly gained wide prevalence. This race had been known to exist in the United States as early as 1939 (14) and possibly was present earlier (16). In Canada, race 15 had occurred sporadically since 1919 (4) but the first isolate definitely identified as race 15B was found in Manitoba in 1946. Since 1950, it has been the predominant physiologic race in Canada, with its greatest concentration in the Prairie Provinces.

BIOTYPES

The outbreak of race 15B in 1950 forcibly called attention to the fact that pathogenic variants of known races may be economically more important than the original types of these races. Such variants have been referred to so commonly as "biotypes" that it seems necessary to retain this term. It seems desirable, however, to have a generally accepted concept of its meaning and of its relation to the term physiologic race. For stem rust of wheat the term "physiologic race" signifies a strain of the rust identifiable by its infection types on the standard differential hosts according to the procedure recommended in the key for the identification of physiologic races of *Puccinia graminis* f. sp. *tritici*.*

The term "biotype" has been used in the literature in two somewhat different senses: (i) for variants of a race that can be distinguished from its described type by minor but readily observable deviations in infection types produced on the standard differential hosts; (ii) for variants of a race that can be distinguished from the original type of the race on hosts other than the standard hosts. Some biotypes, such as 15B, appear to qualify under both the above categories, although that biotype is most readily identified by its infection type on varieties, such as Lee, that are not included in the standard hosts.

There has been a tendency to think of a biotype, in the abstract, as an ultimate and indivisible unit. It seems impracticable to try to reconcile this concept with "biotype" as it has been used in rust work because it is well known that strains thus designated by rust investigators are subdivisible into further pathogenic units.

FACTORS INFLUENCING RACE DISTRIBUTION

The factors influencing the rise and fall in the prevalence of races are by no means clearly understood. Barberry bushes, though greatly reduced in number by the vigorous campaign of eradication which has been in progress since 1918, may still occasionally produce new races by hybridization. The parts that mutation and the introduction by air currents of spores from far-off areas play in the origination of races are but little

*A new revision of this key is in course of preparation. At the time of writing the latest version of the key is that of 1944: Identification of physiologic races of *Puccinia graminis tritici*. E. C. Stakman, M. N. Levine and W. Q. Loegering. U.S.D.A. Bur. Entomol. and Plant Quarantine, E-617, May, 1944. The standard differential hosts comprise the varieties Little Club, Marquis, Reliance, Kota, Arnautka, Mindum, Spelmar, Kubanka, Acme, Einkorn, Vernal and Khapli.

understood. Once a new race has come into being, it is generally accepted that it can persist in the uredial stage by overwintering in southern Texas and in regions farther south. Following overwintering, there is an annual northward movement of the rust into the spring-wheat areas of the northern States and Canada. This is almost certainly followed in the late summer and autumn by a southward movement of rust spores from these northerly regions to the southern states. It is unknown how important this southward movement is. The postulation that it does exist helps to explain the persistent survival for many years of the prevalent races. If such a southward movement of spores is of significance, it follows that the selective effect of wheat varieties in the spring wheat area is an important factor in shaping the pathogenic characteristics of the race population.

The possible selective effect of some of the wheat varieties that have been grown in western Canada and the north-central United States will be considered briefly. Red Fife was the most widely grown wheat in this region from the beginning of wheat cultivation until it was displaced, about 1912, by Marquis which was widely grown until 1935. Red Fife and Marquis, which is a derivative of it, have virtually the same reaction to stem rust races (9). Despite the fact that these varieties are more or less resistant to nearly half of the known races of wheat stem rust they were, nevertheless, susceptible to the races most widely prevalent in the northern states and western Canada when physiologic races were first studied. It seems likely that these wheats had exercised a selective effect on the rust during the period of 35 or more years that they were grown before the discovery of physiologic races, about 1916. Another probable influence of wheat varieties on rust races is the selective effect of certain varieties of *Tirticum durum* that came to be widely grown in the Dakotas, Minnesota, and southern Manitoba about, or shortly before, 1920. Most of the races that were commonly collected in the Prairie Provinces from 1919 to about 1930, such as races 17, 21, 11, 34, were virulent to the widely grown durum varieties Mindum and Kubanka, and other common races such as 18, 36 and 49 were somewhat virulent to Kubanka though not to Mindum.

It has been mentioned above that the high susceptibility of the variety Ceres may have been a factor favouring the spread of race 56. This variety and Marquis, which constituted most of the spring-wheat acreage in the early thirties, were very congenial hosts to this race. The rust epidemic of 1935 and the production at about the same time of rust-resistant wheats resulted in a great reduction in the acreage sown to Marquis and Ceres and a shifting of the centre of their remaining acreage westwards into Montana and the western parts of the Dakotas (1). These varieties, especially Marquis, have never been eliminated in Montana or in the adjacent Canadian province of Alberta where more than one million acres of Marquis were still grown in 1950 (2). Since race 56, even after the outbreak of race 15B, has been a common race in Alberta, though not in areas farther east, it seems probable that fields of Marquis and other susceptible wheats provide a path for its northward spread and an opportunity for its survival.

One of the factors favouring the establishment and persistence of race 15B was the large acreage in the Dakotas devoted to durum wheat. Varieties such as Mindum, Carleton, and Stewart, which had been rust-resistant prior to 1950, were severely rusted in that year. The formerly rust-resistant bread wheats were less congenial hosts but, nevertheless, rusted considerably. The susceptibility of the wheat varieties grown, together with a retarded growing season in the spring wheat area which permitted rust development far into September, provided the conditions necessary for a great increase of urediospores of race 15B. This one race in fact, accounted for no less than 55.8 per cent of Canadian isolates o stem rust in 1950. A southward drift of spores from the vast amount o inoculum produced in the spring wheat areas may well have been the chief factor in the subsequent persistence of this race.

USE OF DIFFERENTIAL HOSTS

Physiologic races are identified primarily to keep the plant breeder informed as to changes in the pathogenic characteristics of the rust against which his breeding program is directed. His principal concern is with the effect of new physiologic races or biotypes on the plant breeding material with which he works. It is, therefore, necessary that the study of physiologic races should be closely related to studies of the reaction to rust of the plant breeder's materials including, particularly, the sources of resistance currently in use. This could be done by incorporating in the differential hosts the varieties in which the plant breeder is chiefly interested. But as these varieties change from time to time this course would lead to frequent changes in the composition of the differential hosts and would also lead to the use of different assortments of hosts in different regions.

When the standard differential hosts used for stem rust race indentification were selected they were fitted to the requirements of the plant breeder by the inclusion in them of varieties in cultivation at that time and others then useful as sources of resistance. Although the standard hosts no longer have much practical value for the breeder they have, nevertheless, been retained by most of those who study stem rust races in this and other countries. They serve to record changes that occur in the pathogenicity of the rust from time to time but frequently the changes they record are not those of most practical significance for the breeding of resistant varieties. To detect such pathogenic changes in the rust it is necessary to employ the actual sources of resistance in use by the wheat breeder. In Canada, and elsewhere, the relationship between race identification and the needs of the breeder has been maintained by the use of accessory hosts. The variety Lee has been used in the United States and in Canada to differentiate race 15B from race 15. At Winnipeg, Man., the variety McMurachy, in use by Canadian plant breeders as a source of resistance to race 15B, was used as an accessory host. For several years it remained an accessory rather than a differential host because no stem-rust cultures virulent to it were found until 1952 when a single large pustule was seen on a plant of McMurachy inoculated with a collection of rust from Regina, Sask. At that moment McMurachy became a differential

host because its use enabled the race investigator to distinguish a new biotype of race 15B (that is, race 15B-Can. 3), from other specimens of that race. This new biotype may be of little or no interest to rust investigators who have no concern with the type of rust resistance possessed by McMurachy but it is of great potential importance for that type of resistance.

In Australia, it has been found necessary to use the varieties Eureka and Yalta to distinguish between certain pathogenic strains that have become economically important in recent years. Eureka differentiates between races 126 and 126B by its immunity to the former and susceptibility to the latter. Eureka and Yalta, jointly, make it possible to subdivide race 222 into the three units 222AA, 222AB, and 222BB, as follows (19):

	Eureka	*Yalta*
222AA	0	0
222AB	0	4
222BB	3	4

The two varieties just mentioned have been used in conjunction with the standard differential hosts. In some countries, however, the practice has grown up of largely or entirely dispensing with the standard differential hosts and depending on the use of locally improvised varietal assortments for the determination of parasitic strains of the rust. In Kenya Colony, stem rust strains have been differentiated chiefly by the reaction of wheat varieties in use in the local plant breeding program and have been recorded by local designations, as K1, K2, etc. In the earlier work (6, 7), physiologic race determinations were also carried out on the standard differential hosts e.g., strains K1, K2, K3, and K4 were found to correspond with races 21, 17, 34, and 116, respectively. The virtual abandonment of the standard differential hosts was probably influenced by the fact that strains K4 and K5 were identical with race 116 but could be distinguished from one another by the reaction of the variety K. 58 (5). More recent records (18) indicate the differentiation of rust strains by means of the reaction of a number of locally produced and a few imported wheat varieties.

The proposal that separate groups of differential varieties be used in different ecologic regions has been advanced by da Silva (11), who considers that a fixed group, such as the present standard differential varieties, does not satisfy the requirements of wheat breeding programs. According to this proposal, the standard differential varieties might be used for reference so as to maintain historical continuity and to permit some comparison of the rust strains present in different ecologic regions. This scheme envisages a permanent series of differential hosts (the standard varieties now in use) and a changeable series, which can be adjusted from time to time to the practical needs of a given rust (ecologic) region. Thereby the confusion which would inevitably result from consecutive modifications of the standard differential series would be avoided. Strains identified by means of a changeable, regional series of differential hosts could be tested on the standard hosts to determine to which of the physiologic races they correspond.

TABLE 3.—INFECTION TYPES PRODUCED ON ACCESSORY DIFFERENTIAL HOSTS BY BIOTYPES OF RACES 15B, 29, 48 AND 56

Race and biotype	Lee	Golden Ball	Selkirk	McMurachy	Sel. 131	Kenya Farmer
15B	3 to 4	2+	1 to X−	1 to X−	0;	1 & N
15B-Can. 3	3 to 4	2+	3 to 4	4	0;	1 & N
15B-Can. 4	3 to 4	4	1 to X−	1 to X−	0;	1 & N
29-Can. 1	1	4	4−	4	4−	1 & N
29-Can. 2	1	2+	4−	4	4−	1 & N
29-Can. 3	1	4	0;	0;	0;	1 & N
29-Can. 4	1	4	0;	0;	0;	1 & N
48A	0;	4	2	4	4	1 & N
56	0;	2	0;	0;	1	1 & N
56-Can. 1	1	2	1*	4	1	1 & N

*Race 56-Can. 1 produces a 3+ type of infection on about half the plants of Selkirk.
NOTE: Selkirk and McMurachy are usable as differential hosts for distinguishing isolates of race 15B only at moderate or low temperatures. At higher temperatures all isolates of race 15B tend to produce infection types X+ or 3 to 4.

An alternative to Dr. da Silva's proposal would be the adoption of a set of accessory hosts generally acceptable to the rust workers in all countries in which race identification is carried out. Such a development would have the advantage of permitting comparison of work performed in different countries. The obstacles, however, may prove to be insuperable, for the simple reason that the rust worker in a given region must be guided in his selection of accessory differential hosts by the sources of resistance used in plant breeding programs in his region; and in this work he must be able to respond quickly to the requirements of a breeding program.

In the operation side by side of a permanent (standard) and a changeable (accessory) set of differential hosts it seems likely that frequent references would have to be made to the standard differential hosts to establish any reliable relationship between the rust strains identified by means of the two sets. It is well known that two or more biotypes of a given race can be identified by means of suitable accessory hosts. Conversely, rust samples that appear to be one and the same strain when identified on accessory hosts may be found, on reference to the standard differential hosts, to be one or another of several different races. Consequently, if a rust investigator classifies his rust cultures into groups according to the reaction of accessory hosts and then refers one or two representatives of each group to the standard hosts, he may acquire misleading evidence as to the relationship of these rust strains to the standard races. It is obvious, therefore, that frequent reference to the standard hosts will have to be made if any exact knowledge is desired of the relationship of the two categories of rust strains.

TABLE 4.—PREVALENCE OF BIOTYPES OF RACES 15, 29, 48 AND 56 IN CANADA, 1952 TO 1955, EXPRESSED IN PER CENT OF TOTAL RACE ISOLATES STUDIED

Race and biotype	1952	1953	1954	1955
15B	83.1	80.1	75.9	61.1
15B-Can. 3	0.3	0.3	1.7	3.3
15B-Can. 4	5.2	2.0	0.8	1.6
29-Can. 1	0	0	5.8	4.9
29-Can. 2	0	0	1.9	1.0
29-Can. 3	0	2.3	0.6	0.3
29-Can. 4	0	0	0	0.3
48A	0	0	3.9	5.2
56	8.1	9.1	4.2	13.4
56-Can. 1	0	0	0.3	0.7

The present use of accessory differential varieties at the Plant Pathology Laboratory, Winnipeg, Man., is indicated in Table 3.

These varieties, except for Sel. 131, are either currently cultivated varieties such as Lee and Selkirk, or varieties used by the plant breeders of the Cereal Breeding Laboratory, Winnipeg, Man., as sources of stem rust resistance, such as Golden Ball, McMurachy and Kenya Farmer. The only variety that is not a differential host is Kenya Farmer. This variety is, however, the most important of the accessory hosts, for practical purposes, because it has been used extensively as a source of resistance in the breeding program. When a strain is found that can attack this variety, it becomes a differential host. Sel. 131, a sister strain of the American variety Bowie, is in use because it is an effective differential host containing, apparently, resistance from Kenya 58. Sel. 131, therefore, serves to call attention to rust strains against which the Kenya 58 type of resistance is ineffective.

New accessory varieties will undoubtedly be introduced in future years. The factors that will determine which varieties are added are: (i) important varieties in cultivation; (ii) new sources of resistance; (iii) new knowledge concerning genetic factors for resistance contained in particular varieties. The last factor will become progressively more important as more knowledge is gained concerning the genetic determiners of rust resistance.

Table 4 shows the prevalence of the biotypes described in Table 3. The distribution of the biotypes is probably influenced by the distribution of the varieties in cultivation. Race 15B-Can. 3, which is more virulent to the variety Selkirk than other known biotypes of race 15B, has been found infrequently in the general rust survey but has been isolated chiefly

TABLE 5.—PHYSIOLOGIC RACES OF WHEAT STEM RUST ISOLATED FROM COLLECTIONS OF AECIA 1944-1954

Race	Number of isolates
1	1
15	3
15B	2
16	1
21	1
27	1
31	1
34	1
38	1
56	2
69	1
87	1
88	1
111	1
179	1
185	1
208	1
Total	21

from rust found on that variety. It is probable that the varieties in cultivation in 1954 in the United States and Canada influenced the distribution of races 29 and 48A in that year. Both races occurred in the southern States early in the summer and later were frequently collected in the eastern States (17). In Canada, they were found sparsely in the Prairie Provinces but abundantly in Ontario and Quebec where they were responsible for the first heavy stem rust infection ever to occur on the variety McMurachy in the rust nurseries. The scarcity of these races in the Prairie Provinces is probably due to the resistance of the widely grown varieties Thatcher, Redman and Lee and varieties with similar resistance grown in the adjoining American States.

RACES DERIVED FROM INFECTED BARBERRY

During the period 1944 to 1954 studies were made each year, except in 1950 and 1951, to determine the relative prevalence of the different varieties of stem rust on infected barberry in Canada. As barberry is extremely scarce in the Prairie Provinces nearly all collections of aecia were obtained from eastern Canada where the plant is more readily found.

Of the 282 isolates of the different varieties of stem rust only 19 or 6.7 per cent belonged to the variety *tritici*. Other stem rust varieties present were *secalis*, 139 isolates (49.3 per cent); *agrostidis*, 65 isolates (23.0 per cent); *avenae*, 48 isolates (17.0 per cent); and *poae*, 11 isolates (3.9 per cent). The relatively small number of isolates of wheat stem rust is perhaps chiefly due to scarcity of wheat and grasses susceptible to wheat stem rust in the areas from which the collections of aecia came.

The race analysis of the 19 isolates of wheat stem rust is given in Table 5. Seventeen races were identified from 19 wheat stem rust isolates, or one race per 1.117 isolates. In comparison, the 4826 isolates of wheat stem rust from cereals and grasses (Tables 1 and 2) were resolved into 71 races, or one race per 67.971 isolates. Comparative figures given by Stakman *et al.* (12) are 1 race per 4 collections of aecia and 1 race per 100 collections from cereals and grasses. Though the number of isolates studied is small the results, nevertheless, indicate the great pathogenic variability of rust derived from aecia.

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DDT AND DDD RESIDUES ON TOMATOES PROCESSED INTO JUICE[1]

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ABSTRACT

Experiments were carried out in 1954 and 1955 in which tomatoes that were field-treated with DDT[3] or DDD[3] were processed into juice by commercial procedures, and components were analysed for residues of these compounds. In 1954, four sprays were applied of DDT at 1.25 and at 2.5 lb. per acre and of DDD at 1.5 lb. per acre; in 1955, six sprays of DDT and of DDD at 1.5 lb. and at 3.0 lb per acre. Residues in the juice did not exceed 0.13 parts per million. Approximately 80 per cent of the residues were removed during washing and most of the remainder was concentrated in the waste.

INTRODUCTION

In southwestern Ontario sustained hot, dry weather in August and September may have a serious effect on the tomato crop by favouring outbreaks of the corn earworm or tomato fruitworm, *Heliothis zea* (Boddie). Corn, the natural host plant of this pest in Ontario, matures early and apparently loses its attractiveness to the earworm. In late August and in September moths from the south enter southwestern Ontario and, instead of ovipositing on the drying corn silks, usually lay their eggs on the ripening tomato crop. Newly hatched larvae burrow into the fruits and complete their development, often undetected, until the tomatoes are examined at the grading station. In 1953 approximately 12,000 acres of tomatoes were infested and canning companies were forced to cease processing prematurely because of this condition.

Since insect fragments are not permitted in processed tomato products, it is most important that insecticides be applied as soon as conditions favour an earworm infestation. Then it is recommended that DDT or DDD at 1.5 lb. per acre be included with the fungicide sprays from mid-August to harvest. This is a report on investigations in 1954 and 1955 to determine the total residue present after regular commercial washing, where the residue is concentrated, and whether the residue of DDT or DDD in the juice remains below the tolerance of 7 p.p.m. established in the United States (2,).

In California, Michelbacher *et al.* (3) did not detect any insecticide residues in juice made from tomatoes that had received two applications of DDT or DDD at approximately 1.75 lb. per acre per application. In their experiment the treatments were applied by hand sprayer. The tomatoes were picked on the day of the last application, washed, and processed into juice with home equipment. The waste contained 2.7 and 2.9 p.p.m. of DDT and DDD respectively.

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[3]DDT, 1:1:1:-trichloro-2:2-bis (*p*-chlorophenyl) ethane;
DDD, 1:1 dichloro-2:2-bis (*p*-chlorophenyl) ethane.

METHODS

In 1954 experimental plots were sprayed with 1.25 and 2.5 lb. of DDT per acre on July 23 and August 5, 17, and 26. Sprays of 1.5 lb. of DDD per acre were applied on July 6 and 16 and August 2 and 18. Bushel lots were picked at random from the DDT-treated plots on September 22 and from the DDD-treated plots on September 21. The tomatoes from each treatment and the checks were washed and processed into juice on September 23 by regular commercial methods in all operations. Twenty-eight days elapsed between the last spray and the processing of the DDT-treated tomatoes, and 36 for the DDD-treated tomatoes.

Since the danger of an earworm infestation exists until harvest, the experiment was repeated in 1955, the tomatoes being harvested and washed on the day of the final spray. They were processed into juice the following day. Sprays of 1.5 and 3.0 lb. of DDT or DDD per acre were applied on July 11 and 21, August 2, 12, and 22 and September 6. By including an insecticide in each of the regular fungicide sprays and by reducing to one day the interval between the last spray and processing, optimum conditions for residues were provided.

All sprays were applied with commercial, tractor-drawn equipment delivering 120 to 150 gal. per acre at 450 to 500 lb./sq. in. Excellent coverage of vines and fruits was obtained.

Random samples of whole tomatoes from each treatment were tumbled in glass jars with chloroform to remove the insecticide residue. The juice from the remaining whole tomatoes of each treatment was canned and the waste frozen in waxed cardboard containers. For analyses the waste was spread in glass trays and dried at room temperature before extracting with chloroform in Soxhlet extractors. Each juice sample was poured on to a 20″ × 20″ sheet of double weight filter paper, suspended in mid-air by clips, and dried overnight at room temperature. It was then folded into a compact roll, placed in a Soxhlet extractor, and the insecticide residues extracted with chloroform.

TABLE 1.—DDT AND DDD RESIDUES IN PARTS PER MILLION ON WHOLE TOMATOES AND IN WASTE AND PROCESSED JUICE AFTER FOUR SPRAY APPLICATIONS, CHATHAM, ONT., 1954

Insecticide	Toxicant per acre, lb.	Whole tomatoes		Waste		Juice
		Before washing	After washing	Wet	Dry	
DDT[1]	1.25	0.27	0.22	2.9	9.7	<0.02
DDT	2.5	0.72	0.19	3.1	11.9	<0.02
DDD[2]	1.5	0.08	0.03	1.2	5.6	<0.02

[1]50% wettable powder; Canadian Industries Limited, Montreal, Que. 28 days between last sprays and processing.

[2]50% wettable powder; Canadian Industries Limited, Montreal, Que. 36 days between last spray and processing.

The extracts were decolorized and analysed for DDT and DDD by the colorimetric method of Schechter and Haller as modified by Downing and Norton (1). All analyses were performed in triplicate.

RESULTS AND DISCUSSION

Table 1 shows that DDT and DDD residues on whole tomatoes, before washing, are negligible when the period between the last spray and processing approximates 28 and 36 days respectively. Such small residues would probably be ineffective against an outbreak of the earworm near harvest. In 1954 no measurable amount of either insecticide was present in the juice, the lower limit detectable by the procedure used being 0.02 p.p.m.

Table 2 shows that commercial washing removed approximately 80 per cent of the spray residues irrespective of the rate of application. In the larger processing plants in southwestern Ontario, wash water is not recirculated. When recirculation is practised the accumulation of insecticide residues in the water might alter results of similar experiments. The remaining 20 per cent of residue was concentrated in the waste, and, more especially on the skins (analysis of chili sauce, which contains tomato seeds, showed no residue of insecticide from treated tomatoes). Since a high concentration of residue was present in the waste, its disposal is of some concern. In southwestern Ontario the waste is normally trucked from the processing plant and spread on fields for whatever fertilizer value it has. This is probably the safest method of disposal. Feeding it to animals, although not widely practised, should be discontinued.

The insecticide residue in the tomato juice in both experiments was well below the United States tolerance of 7 p.p.m. Hence juice processed commercially from tomatoes sprayed with DDT or DDD throughout the growing season is not adulterated by residues to an extent that would constitute a health hazard.

TABLE 2.—DDT AND DDD RESIDUES IN PARTS PER MILLION ON WHOLE TOMATOES AND IN WASTE AND PROCESSED JUICE AFTER SIX SPRAY APPLICATIONS, CHATHAM, ONT., 1955[1]

Insecticide	Toxicant per acre, lb.	Whole tomatoes			Waste		Juice
		Before washing	After washing	Percentage removed	Wet	Dry	
DDT	1.5	0.53	0.15	72	1.9	8.7	0.02
DDT	3.0	5.68	1.08	81	25.4	106.2	0.06
DDD	1.5	1.78	0.37	79	8.3	37.9	0.04
DDD	3.0	5.41	0.67	88	12.6	71.2	0.13

[1]Interval of one day between last sprays and processing.

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SAWFLY RESISTANCE IN WHEAT

II. DIFFERENCES BETWEEN WHEAT GROWN IN THE GREENHOUSE AND ON IRRIGATED LAND[1]

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ABSTRACT

The resistance of seven varieties of wheat to the wheat stem sawfly (*Cephus cinctus* Nort.) was tested in the greenhouse and on irrigated plots. In five of the seven varieties tested, namely, Rescue, H46146, Golden Ball, Red Bobs and Thatcher, the percentage of infested stems that were cut by sawflies was significantly higher in plants grown in the greenhouse in either summer or winter than in plants grown under irrigation in the field. In the other two varieties, H4191 and Melanopus, results were similar but the differences were not significant. This lower resistance of plants grown in the greenhouse was associated with a decrease in the percentage of tunnelled stems in which the older larvae had died. In percentage of infested stems cut, no significant differences were found between the varieties grown in the outdoor soil bins and those on adjacent irrigated land. In other 2-year tests on irrigated land, the variable resistance of wheat was apparently associated with variations in percentage of tunnelled stems in which the older larvae had died. Although stem solidness is usually associated with resistance on dry land, it appears that this characteristic alone cannot be relied on as a measure of sawfly resistance in a given variety when grown in diverse environments.

INTRODUCTION

In the study of the resistance of wheat to the wheat stem sawfly (*Cephus cinctus* Nort.) it is sometimes convenient to carry out experiments in the greenhouse or on irrigated plot land. It is important to know whether the results of these experiments will be directly applicable to dry-land field conditions. The purpose of the present experiments was to obtain information on sawfly resistance of wheat grown in the greenhouse and on irrigated plot land and to try to discover whether the differences were due to death of the older larvae or of eggs and very young larvae.

MATERIALS AND METHODS

In these experiments the same seven varieties of wheat were used as in the previous tests (2), namely, the bread wheats, Thatcher, Red Bobs, Rescue, Hybrid H4191 and Hybrid H46146, and the durum wheats, Golden Ball and Melanopus.

For the tests of resistance in the greenhouse the wheat was seeded in soil bins, 32 × 32 × 8 in. in size, containing mixed top-soil. The winter crop was seeded in two replicates during the first two weeks of January. The summer crop was seeded on the following dates: May 26 to 30, 1950; June 15, 1951; May 26 to 28, 1952; and June 1, 1953. When the wheat reached a stage between shot blade and flowering, a cage was placed over it and 20 pairs of sawflies were introduced. Two weeks later the cage was removed. When the wheat was fully ripe and all cutting of

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the stems by sawflies was completed, the material was dug up and counts were made as described earlier (2) to determine the percentage of infested stems cut, the percentage of infested stems in which the eggs and young first instar larvae survived and the percentage of tunnelled stems in which the larvae survived. As in the earlier report (2), the last category includes only those larvae that produced macroscopically visible tunnels.

Two outdoor tests were made in duplicate simultaneously with the summer greenhouse test. For the outdoor plot test, the wheat was seeded on irrigated land. For the outdoor soil-bin test, the wheat was seeded in soil bins similar to those used in the greenhouse. These bins were placed outdoors next to the plots and in both tests the wheat was watered with a hose as required. Soil from the same source was used in the outdoor soil-bin test and in the greenhouse test carried out in the summer time. In these plots, also, 20 pairs of sawflies were released under cages and counts were made similar to those in the greenhouse experiments.

For additional experiments on irrigated land the plots were seeded in a different location from the outdoor plots described above. This plot land had a history of irrigation where water had been supplied as required for plant growth for many years previous to these tests. In both 1950 and 1951 these experiments were set up with seven varieties in three or four replicates in a randomized block design and stubs were transplanted from an infested area into the spaces between the rows of wheat. Ten stubs were placed beside each foot of test row. In 1950, these plots were watered with a hose as required, but in 1951 no water was supplied as it was a very rainy year (17.3 inches total precipitation April 1 to August 31). The mature stems were examined for the results of sawfly activity as described above.

The data from experiments on dry land plots in 1950, 1951, and 1952 are taken from experiments described in detail previously (2). The data for 1954 and 1955 are taken from plots used as controls in experiments on the effect of nitrogenous fertilizer on sawfly resistance. These plots were arranged in a randomized block design and a natural sawfly infestation was used.

Stem solidness ratings were made by the method of Larson*. In this method transverse cuts of the stems were made with the scissors at the middle of every internode and also in the uppermost internode at points approximately one-quarter and three-quarters of the length of the upper internode below the ear. When the stem was found to have a thin wall and large central cavity, a rating of *1* was given to it; but when there was no central cavity and the stem was solid, a rating of *5* was given. Values of *2*, *3* and *4* were given for intermediate conditions of stem-solidness. In the present study the values for each position of the cut in twelve uninfested stems selected at random from the test plot were averaged and this average was multiplied by seven, the number of cuts usually made in each stem.

*Larson, R. I. Aneuploid analysis of the inheritance of solidness in common wheat. Unpublished Ph.D. thesis, University of Missouri. 1952.

The data on sawfly resistance and stem solidness were subjected to the analysis of variance. Where percentages were involved the arc sine transformation was used. The irrigated-plot data for the two years were analysed separately. The other data were combined as indicated in the tables. The sums of squares for treatments, years and interaction were determined. When a significant interaction was found it was used to test the significance of the treatment differences.

RESULTS

Sawfly Resistance in the Greenhouse

Data on the percentage of infested stems cut in greenhouse grown wheat as compared with the percentage of those cut in wheat grown outdoors are summarized in Table 1.

In five out of the seven varieties the percentage of infested stems cut in the crop grown in the greenhouse was significantly higher than that of the plants grown outdoors. Although not significant, the differences between greenhouse- and outdoor-grown crops of H4191 and Melanopus were of the same order of magnitude as in the other varieties. Rescue showed a significantly higher percentage of infested stems cut when grown in the greenhouse in the winter than in the summertime. The other varieties did not show this difference. No significant differences were found between the crop grown in the outdoor soil-bins and the one on adjacent plot land. In the present tests of sawfly resistance there were no significant differences between varieties in percentages of infested stems cut either when they were grown in the greenhouse or outdoors during the last two years of test common to all varieties.

Although the data are not presented here, in six out of the seven varieties no significant differences between treatments were found for the

TABLE 1.—EFFECT OF GREENHOUSE AND OUTDOOR IRRIGATED CONDITIONS ON THE PERCENTAGES OF INFESTED WHEAT STEMS CUT BY SAWFLIES

Variety	Number of years tested	Averages of transformed percentage values				L.S.D. treatments
		Winter greenhouse	Summer greenhouse	Outdoor soil bins	Outdoor plots	
Bread wheats						
Thatcher	4	66	71	25	25	5*
Red Bobs	3	65	62	26	23	10*
Rescue	4	63	46	19	15	12*
H4191	2	58	55	22	20	—
H46146	2	54	50	19	19	12*
Durum wheats						
Melanopus	2	58	54	24	28	—
Golden Ball	4	49	49	10	19	13*

*Differences between treatments significant at 1% level. No significant differences were found between varieties for last two years of test common to all varieties.

TABLE 2.—EFFECT OF GREENHOUSE AND OUTDOOR IRRIGATED CONDITIONS ON THE PERCENTAGES OF TUNNELLED WHEAT STEMS THAT WERE CUT BY SAWFLIES

Variety	Number of years tested	Averages of transformed percentage values				L.S.D. treatments
		Winter greenhouse	Summer greenhouse	Outdoor soil bins	Outdoor plots	
Bread wheats						
Thatcher	3	73	72 (71)	28	25	8*
Red Bobs	3	77	63 (63)	26	23	11*
Rescue	3	69	58 (52)	26	16	17*
H4191	2	62	63 (63)	26	22	—
H46146	2	60	52 (52)	24	22	12*
Durum wheats						
Melanopus	2	72	58 (58)	27	28	13*
Golden Ball	3	60	67 (74)	10	27	13*
L.S.D.**		—	— (10)	—	—	

*Differences between treatments significant at 1% level.
**For the last two years of data common to all varieties, significant differences between varieties were found only in the summer greenhouse test. The difference shown applies to the averages for the last two years. These figures are given in brackets.

percentage of stems showing survival of eggs and very young larvae. In Red Bobs, however, the survival of eggs and very young larvae was lower (significant at 5 per cent level) in the winter greenhouse test than in any of the other three tests.

When the data on the percentage of tunnelled stems that were cut were examined it was found that significantly greater resistance to tunnelling larvae occurred in six of the seven varieties grown outdoors than in these same varieties grown in the greenhouse (Table 2). The percentage of tunnelled stems that were cut was similar in both winter and summer crops grown in the greenhouse for all varieties, except Melanopus and Red Bobs. Similarly, except for Golden Ball, there were no significant differences in percentage of tunnelled stems that were cut between crops grown outdoors on irrigated plots and those grown in adjacent soil bins.

The data indicate that the greater percentage of infested stems cut in the greenhouse-grown crops as compared with the outdoor-grown crops was largely the result of the smaller number of uncut tunnelled stems rather than a smaller number of infested stems in which the eggs and very young larvae failed to survive. The similarity in the sawfly resistance of crops grown in soil bins outdoors to the resistance of those grown in adjacent plots indicates that the increase in percentage of infested stems that were cut in the greenhouse was not due to some factor arising from the use of soil bins for the greenhouse crop.

Sawfly Resistance on Additional Irrigated Plots

The results of tests on sawfly resistance of seven varieties grown on irrigated land in 1950 and 1951 are presented in Tables 3, 4, and 5. There were significant differences between the varieties in 1950 only in percentage

TABLE 3.—EFFECT OF IRRIGATED AND DRY LAND CONDITIONS ON THE PERCENTAGES OF INFESTED WHEAT STEMS CUT BY SAWFLIES

Variety	Averages of transformed percentage values							
	Outdoor plots[1]	Irrigated plots		Dry land plots				
		1950	1951	1950	1951	1952	1954	1955
Bread wheats								
Thatcher	25	63	27	59	68	60	55	61
Red Bobs	22	55	30	63	67	58	48	62
Rescue	15	50	25	30	55	36	35	54
H4191	15	41	27	43	51	39	—	—
H46146	16	46	19	32	55	32	35	44
Durum wheats								
Melanopus	24	60	43	43	42	40	61	35
Golden Ball	19	30	43	46	42	46	47	36
L.S.D.	—	—	7	5	4	4	5	4

[1]Four years' data from same irrigated plots that were used for experiments comparing plants grown in the greenhouse with those grown outdoors.

TABLE 4.—EFFECT OF IRRIGATED AND DRY LAND CONDITIONS ON THE PERCENTAGE OF INFESTED STEMS WITH EGGS AND YOUNG FIRST INSTAR LARVAE SURVIVING

Variety	Averages of transformed percentage values							
	Outdoor plots[1]	Irrigated plots		Dry land plots				
		1950	1951	1950	1951	1952	1954	1955
Bread wheats								
Thatcher	76	74	90	74	87	85	90	77
Red Bobs	83	74	88	79	88	85	89	82
Rescue	64	66	74	51	66	54	85	64
H4191	64	53	73	53	65	52	—	—
H46146	63	60	70	42	60	53	81	55
Durum wheats								
Melanopus	74	67	83	54	59	59	85	49
Golden Ball	65	58	76	65	51	63	88	50
L.S.D.	—	8	6	17	4	7	4	4

[1]Four years' data from same irrigated plots that were used for experiments comparing plants grown in the greenhouse with those grown outdoors.

of infested stems with eggs and young first instar larvae that survived. It is possible that other differences would have been found if more than three replicates had been used. In 1951 significant differences were found between varieties in percentage of infested stems cut, percentage of infested stems with eggs and young first instar larvae that survived, and percentage of tunnelled stems that were cut. In general, except for Golden Ball, in the varieties tested on irrigated land the percentage of infested stems that were cut was markedly lower in 1951 than in 1950. In agreement with the experiments on dry land, the percentage of stems showing egg survival was higher in Thatcher and Red Bobs than in the other varieties in both years (Table 4). In 1951 the mortality of the older larvae was quite similar for both the solid- and hollow-stemmed bread wheats and these as a group were significantly more resistant than the durums. This lower larval survival resulted in a significantly lower percentage of stems cut in the bread wheats. The 1951 data for stems that showed survival of older larvae (Table 6) exhibited between replicate 1 and 4, a pronounced

TABLE 5.—EFFECT OF IRRIGATED AND DRY LAND CONDITIONS ON THE PERCENTAGE OF TUNNELLED WHEAT STEMS THAT WERE CUT BY SAWFLIES

Variety	Averages of transformed percentage values							
	Outdoor plots[1]	Irrigated plots		Dry land plots				
		1950	1951	1950	1951	1952	1954	1955
Bread wheats								
Thatcher	25	75	28	64	68	60	55	64
Red Bobs	22	51	31	66	67	56	47	64
Rescue	16	56	26	40	64	46	33	65
H4191	18	54	29	57	65	53	—	—
H46146	19	57	21	55	64	42	36	58
Durum wheats								
Melanopus	26	61	44	57	52	48	63	50
Golden Ball	23	50	46	52	59	54	47	50
L.S.D.	—	—	7	18	6	6	5	5

[1]Four years' data from same irrigated plots that were used for experiments comparing plants grown in the greenhouse with those grown outdoors.

TABLE 6.—SAWFLY RESISTANCE OF SEVEN WHEAT VARIETIES GROWN IN 1951 ON A PLOT WITH A HISTORY OF IRRIGATION

Variety	Percentage of infested stems cut in replicate				Percentage of tunnelled stems that were cut by sawflies in replicate			
	1	2	3	4	1	2	3	4
Bread wheats								
Thatcher	33	28	17	9	33	28	17	9
Red Bobs	46	36	16	11	46	36	16	12
Rescue	25	24	17	7	27	25	20	7
H4191	34	20	17	13	41	22	19	13
H46146	25	23	11	0	28	29	12	0
Durum wheats								
Melanopus	38	51	46	52	38	53	47	54
Golden Ball	42	52	42	53	50	55	48	53
Replicate averages[1] for arc sine transformation	36	35	29	24	38	36	30	24

[1]L.S.D. for replicates of percentage infested stems cut is 5; of percentage of tunnelled stems cut is 5. For L.S.D. values between varieties see Tables 3 and 5.

gradient in resistance among the bread wheats but not among the durums. The presence of this gradient, resulting from increased larval mortality in replicates 3 and 4, suggested the existence of some soil factor that affects the resistance of the bread wheats. Previous work (2) showed similar differences in resistance to larval survival on dry-land plots. Further tests on irrigated plots have been delayed until information is available concerning the effects of the mineral nutrition of the wheat plants on their sawfly resistance.

The data in Table 3 allows a tentative comparison to be made of sawfly resistance of wheat on dry land and irrigated land. The data for 1950 irrigated plots are generally similar to the data for dry-land plots, except that significant differences were not obtained with three replicates under irrigation while differences were obtained with three replicates on dry land. However, the data for 1951 irrigated plots and the 4 years of outdoor irrigated plots are quite different from data from dry-land plots.

TABLE 7.—STEM SOLIDNESS OF WHEAT VARIETIES UNDER GREENHOUSE AND OUTDOOR IRRIGATED CONDITIONS

Variety	Number of years tested	Solidness rating[1]				L.S.D.[2]
		Winter greenhouse	Summer greenhouse	Outdoor soil bins	Outdoor plots	
Bread wheats						
Thatcher	3	9 (9)	8 (8)	9 (9)	8 (8)	—
Red Bobs	3	8 (8)	8 (8)	9 (9)	8 (8)	—
Rescue	3	22 (24)	24 (25)	26 (27)	21 (24)	2.4*
H4191	2	16 (23)	18 (27)	19 (29)	17 (26)	—
H46146	2	16 (23)	18 (27)	18 (27)	14 (22)	—
Durum wheats						
Melanopus	2	23 (23)	27 (27)	21 (22)	22(22)	3*
Golden Ball	3	31 (32)	34 (34)	33 (34)	31 (33)	—
Mean of all varieties		(20)	(22)	(22)	(20)	1**
L.S.D.[1]		(4)	(4)	(3)	(3)	

* and ** Differences significant at 5% and 1% level, respectively.
[1]Last two years' data common to all varieties are given in brackets.
[2]Differences between treatments within varieties for number of years tested.

It appears that the sawfly resistance of wheat grown under irrigation may be different from that grown on dry land. In the greenhouse experiments, 4 years' testing with duplicated plots failed to show significant differences between varieties in percentage of infested stems cut.

The data (Table 5) on the percentage of tunnelled wheat stems cut by sawflies shows a high level of resistance among bread wheats grown on irrigated land in 1951 and on outdoor plots as compared with plants grown on dry land.

Stem Solidness and Resistance

The data (Table 7) on stem solidness (Larson's method) indicate only small differences within varieties between crops grown outdoors and in the greenhouse. However, between outdoor and greenhouse crops there were significant differences in the percentage of stems cut (Table 1) and percentage of tunnelled stems that were cut (Table 2). Thus it appears that changes in stem solidness alone do not account for the lower resistance in the greenhouse as compared with outdoors.

In the two irrigated plot tests the normally solid-stemmed bread wheats tended to be more hollow-stemmed in 1951 than in 1950 (Table 8), although the percentages of stems cut were lower in 1951 than in 1950 (Table 3). In 1951 only small differences in percentage of infested stems that were cut were noted between Thatcher, Rescue, and H4191 whereas the difference in stem solidness between Thatcher and Rescue or H4191 was appreciable. These data suggest that there are important factors other than stem solidness affecting the sawfly resistance of crops grown on irrigated plots.

DISCUSSION

The data presented show that the sawfly reaction of wheat grown in the greenhouse differs greatly from that grown outdoors. The difference appears to be caused chiefly by greater survival of the older larvae in plants

TABLE 8.—STEM SOLIDNESS OF WHEAT VARIETIES ON IRRIGATED PLOTS

Variety	Solidness rating	
	1950	1951
Bread wheats		
Thatcher	8	9
Red Bobs	8	9
Rescue	29	26
H4191	29	24
H46146	30	28
Durum wheats		
Melanopus	21	21
Golden Ball	34	33
L.S.D.*	2.8	3.5

*Differences between varieties significant at 1% level in both years.

grown in the greenhouse. This difference does not appear to be due to factors arising from the use of soil bins. Since the varietal reaction of crops grown in the greenhouse either in the summer or winter is similar, it is unlikely that temperature is responsible for the difference although the temperature in the greenhouse in the summer with the windows open was consistently about 10°F. higher than outdoors. It is possible that lower light intensities may be associated with the higher percentage of infested stems cut in the greenhouse compared with outdoors (1). Light intensities in the greenhouse in the summertime are about 75 per cent of those measured outside the greenhouse.

The results of tests on irrigated and dry land indicate that the resistance of wheat to sawflies may not be the same under these conditions. These differences may be connected with soil conditions and the mineral nutrition of the wheat plants.

In a general way, stem solidness in the bread wheats is associated with sawfly resistance on dry land. It appears that this condition does not always apply on irrigated land.

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GENETIC ANALYSES OF CERTAIN CHARACTERS IN COMMON WHEAT USING WHOLE CHROMOSOME SUBSTITUTION LINES[1]

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ABSTRACT

Three sets of substitution lines of the spring wheat variety Chinese with chromosomes from the donor varieties Thatcher, Hope and Timstein were used to study the genetics of awning, earliness, lodging, plant height, spike density, 1000-kernel weight and yield. The various substitution lines, each representing a genotype that differs from that of the recipient variety only with respect to the genes carried by the substituted chromosome, were studied in replicated field trials so that environmental effects on the character in question could be easily removed by appropriate analysis. This permitted a comparison of the genetic effects of individual chromosomes against the standard based on the performance of a population of like genotypes.

Genes conditioning awning were associated with seven chromosomes. Studies of earliness indicated that time of heading is conditioned by (a) major genes that differentiate spring and winter growth habit, and (b) genes that modify the expression of growth habit genes to a greater or lesser extent. Differences in spike density among the lines were due to minor genes only; the same was true for plant height. Lodging, protein content, 1000-kernel weight and yield were found to be conditioned by polymeric or multiple genes on many chromosomes; the effects of these individual genes though small were not usually equal.

Where a substituted chromosome brings about a significant departure in character expression from that of the recipient variety, a method is outlined whereby the number of genes on a particular chromosome can be determined. The merits of the substitution method are discussed, and it is concluded that it is valuable, and gives a high degree of precision in genetic studies of polyploid organisms and that under certain conditions its effectiveness is similar to that of the backcross method for incorporating characters controlled by one or two genes into a given line or variety.

INTRODUCTION

Genetic analyses of quantitative characters in polyploid organisms such as hexaploid common wheat, *Triticum aestivum* L. (emend Fiori et Paoletti) have been difficult, and the results inconclusive. To a large extent, this is caused by duplication of factors which mask or inhibit effects of genes and to the presence of minor or modifying genes which increase the difficulties of correct classification of individual plant segregants.

The aneuploid series developed in common wheat, Sears (23), together with secondary aberrations such as telocentric and isochromosomes, Sears (24), provide a means whereby each of the chromosomes of Chinese Spring (hereafter referred to as "Chinese") may be replaced by the homologous chromosomes of other varieties. The seed from such substitution lines can be increased so that the lines having the different substituted chromosomes of the donor varieties can be compared in replicated field trials with the recipient variety Chinese and with the donor varieties.

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Since each substituted chromosome is present in the more or less uniform genetic background of Chinese, the possibility exists of studying, at least in some cases, the effect of the genes present on the chromosome on quantitative or qualitative characters.

In this investigation three sets of substitution lines of Chinese with chromosomes from the donor varieties Thatcher, Hope and Timstein were used to study awning, earliness, height, lodging, protein content, spike density, 1000-kernel weight, and yield. Lines involving chromosomes XIV and XVII from Thatcher, and chromosomes XIII and XIV from Hope and Timstein, were not available when the study was begun.

REVIEW OF LITERATURE

Cytologic and Cytogenetic Studies of Monosomics and Nullisomics

Cytologic investigations of monosomic (2n-1) plants have been reported in *Nicotiana tabacum*, an allotetraploid with 2n = 48 by Clausen (9) and Clausen and Cameron (10). The entire set of 24 possible monosomics in that species have been isolated, and 18 genes have been located on 9 chromosomes by the use of these monosomics. Investigations of whole chromosome deficiencies have been carried out in common wheat by Love (18) and Nishiyama (20). Sears (23, 24) has isolated all 21 monosomics in the common wheat variety Chinese.

Olmo (21) and Clausen and Cameron (10) have failed to obtain nullisomics in *N. tabacum*. In common wheat, nullisomics have been obtained by Love (18) and Smith, Huskins and Sander (25). Sears (24) has reported that all 21 possible nullisomics have been isolated in Chinese.

The breeding behaviour of monosomics in *N. tabacum* has been studied by Olmo (21). In common wheat the breeding behaviour of monosomics has been studied by Nishiyama (20), Smith, Huskins, and Sander (26), and Sears (23, 24).

Sears in his paper on nullisomic analyses in common wheat (24) has described the four general methods of cytogenetic analysis used in associating certain genes with specific chromosomes. Several genes have been located in varieties of common wheat, through the use of these four methods. Sears (23) using nullisomic analysis located the dominant gene for red seeds on chromosome XVI, genes for awn inhibition on chromosomes VIII and X, and two awn-promoting genes on chromosomes II and XX. He also associated the hemizygous-ineffective recessive gene for square-headedness with chromosome IX and the sphaerococcum gene with chromosome XVI.

Studying F_2 populations from monosomic F_1's, Unrau (30) reported awn suppressors (B_1) on chromosome IX in Hymar and Federation 41 wheats, and recessive alleles of the two awn-inhibiting genes of Chinese on chromosomes VIII and X of Hymar. He found that the dominant genes for red glume colour in Federation 41 and dense spikes in Hymar were associated with chromosomes I and XX respectively. One of two duplicate genes for winter growth habit was associated with chromosome IX of Hymar. Sears (24) associated a gene for pubescent glumes in Indian with chromosome XIV.

The use of chromosome substitution lines in genetic analysis has been discussed by Sears (23, 24). O'Mara (22) studied the effect of substituting a specific *Secale cereale* chromosome for a specific *T. vulgare* chromosome.

Genetic Analyses of Characters Involved in this Study

Awning

Data regarding inheritance of awning have been interpreted in various ways by different investigators. Probably the lack of apparent agreement arises from (1) use of different systems of classification, (2) parental material similar in phenotype but of different genotype, and (3) difficulties in placing segregants in the appropriate genotypic classes.

Tip-awned or awnletted varieties have been found to differ from fully awned varieties by one gene, with fully awned recessive (4, 8, 27, 29). In crosses of awnless with tip-awned or completely awned varieties segregation was found to be more complex. In most studies (4, 6, 7, 14) digenic ratios were obtained with suppression of awns dominant. Clark, Florell and Hooker, (7) reported that as many as four gene pairs were involved in the inheritance of awning. The most extensive studies on the genetics of awning by Watkins and Ellerton (31) have shown that three, or possibly four main loci determine the extent of awn development. They postulated that if any two or all three of the genes Hd, B_1 and B_2 were in the homozygous state, the plant would be awnless; if homozygous for only one dominant pair, it would be tip-awned, and if all three were homozygous recessive, the plant would be fully awned. Using aneuploid methods of analysis Hd, B_1 and B_2 were associated with chromosomes VIII, IX and X respectively, (23, 30). Sears (23) associated two awn-promoting genes with chromosomes II and XX respectively in the variety Chinese.

Earliness

Florell (11) reported monogenic control of earliness. Nieves (19) and Florell (12) found earliness to be controlled by three independent gene pairs. Most investigators claim earliness to be governed by a complex gene relation (14, 29). Usually earliness has been found to be dominant or partially dominant (1, 6, 11, 19, 29); however, Freeman (13) found lateness to be partially dominant.

Plant Height

Few investigations have been conducted on the genetics of plant height.

Nieves (19) reported that tallness was dominant and controlled by two independent gene pairs. Freeman (13), Clark (6), and Torrie (29) found plant height to be controlled by multiple genes and tallness to be partially dominant.

Lodging

Few studies have been conducted on this quantitative character.

Kilduff (17) and Torrie (29) postulated that multiple genes apparently control the inheritance of straw strength. Torrie (29) found partial dominance of strong straw.

Protein Content

Protein, a component of quality, has been studied fairly extensively. Worzella (32) reported the only case of monogenic control of protein content in soft winter wheat hybrids. The majority of reports state that multiple genes control inheritance of protein content (2, 7, 32, 33). Dominance of genes for low protein content was found by Clark, Florell and Hooker (7). Transgressive segregation was reported by Clark and Quisenberry (8).

Spike Density

Although a few investigators (12, 19) report digenic control of spike density, in general most investigators agree that one main gene is responsible for differentiating "club" and "common" spikes in wheat (5, 12, 27, 52). Transgressive segregation was observed by most workers, indicating that one or more minor genes modify the expression of the major gene. Unrau (30), in crosses between Chinese monosomics (lax) and Hymar (dense), associated the gene differentiating dense and lax spikes with chromosome XX. Transgressive segregation indicated that at least one additional gene was modifying degree of density.

Thousand-Kernel Weight

Differences in 1000-kernel weight have been found to be definitely inherited. Monogenic (32), trigenic (16), and multigenic (33) control of the inheritance of this character has been reported.

TABLE 1.—CLASSIFICATION OF AWN EXPRESSION FOR CHINESE, THATCHER, HOPE, TIMSTEIN AND FOR THE THATCHER, HOPE AND TIMSTEIN SETS OF SUBSTITUTION LINES

Substitution lines and varieties	Thatcher set of substitution lines	Hope set of substitution lines	Timstein set of substitution lines
I	Awnless	Awnless	Awnless
II	Awnless	Awnless	Awnless
III	Apically awned	Awnless	Apically awned
IV	Apically awned	Awnless	Awnless
V	Awnless	Awnless	Awnless
VI	Awnless	Awnless	Awnless
VII	Awnless	Awnless	Awnless
VIII	Awnletted	Apically awned	Apically awned
IX	Awnletted	Awnless	Awnless
X	Apically awned	Apically awned	Apically awned
XI	Awnless	Awnless	Awnless
XII	Apically awned	Awnless	Awnless
XIII	Awnless	Awnless	Awnless
XV	Awnless	Awnless	Awnless
XVI	Awnless	Awnless	Awnless
XVII	Awnless	Awnless	Awnless
XVIII	Awnless	Awnless	Awnless
XIX	Awnless	Awnless	Awnless
XX	Awnless	Awnless	Awnless
XXI	Apically awned	Awnless	Awnless
Chinese	Awnless	Awnless	Awnless
Thatcher	Awnletted	—	—
Hope	—	Awned	—
Timstein	—	—	Awnletted

Yield

Yield, a character influenced to a large extent by environmental conditions, has definitely been found to be heritable. Multigenic control only has been observed (3, 6, 29). Transgressive segregation was reported in many cases (7, 8). Both partial dominance of low yield (3, 29) and high yield (6) were observed.

MATERIALS AND METHODS OF PROCEDURE

Description of Parental Varieties

Four varieties of common wheat were involved in the production of the three sets of substitution lines. Chinese was used as the recipient variety in the establishment of all three sets of substitution lines; chromosomes from the varieties Thatcher, Hope, and Timstein were substituted for their homologues in Chinese, and will be referred to as Thatcher, Hope, and Timstein sets respectively.

A description of the varieties with respect to the characters studied is given below. The values in the description for each of the characters studied are 2-year (1953–54) averages. The values for all Chinese characters in this description are averages for Chinese from all three sets and, therefore, will not always correspond to the Chinese values in the tests of the three individual sets of substitution lines. The averages for Thatcher, Hope and Timstein characters are from tests involving these varieties with their respective substitution lines. The Hope and Timstein values correspond to those in Tables 1 to 8, since all Hope and Timstein

Character	Variety			
	Chinese	Thatcher	Hope	Timstein
Awning	Awnless	Awnletted	Awned	Awnletted
Earliness[1]	66.2	57.9	61.3	56.0
Spike density[2]	3.17	2.13	2.15	1.91
Height	midtall (45.1″)	midtall (41.2″)	midtall (44.9″)	short (35.8″)
Lodging resistance[3]	very susceptible (4.0)	very resistant (9.8)	very resistant (9.4)	very resistant (9.7)
Protein content	13.90%	15.00%	13.35%	13.25%
1000-kernel weight	20.6 grams	31.5 grams	36.5 grams	35.6 grams
Yield[4]	473.4 grams	1018.5 grams	892.1 grams*	957.9 grams

*The yield of Hope was determined in 1954 only; however, to make results comparable, the 1953 yield was calculated on the basis that Hope outyielded Chinese in 1953 by the same percentage (84%) as in 1954. The value 892.1 is an average of the calculated 1953 yield and the actual 1954 yield.

[1] Earliness values are average days to head.

[2] Spike density values represent the average number of spikelets per centimetre length of spike.

[3] Lodging resistance values are averages of scores of 1 to 10, with 1 showing complete lodging and 10 showing complete lodging resistance.

[4] Yield values are those for 2-row, rod-long plots.

TABLE 2.—DAYS TO HEAD OF CHINESE, THATCHER, HOPE, TIMSTEIN AND OF THATCHER, HOPE, AND TIMSTEIN SETS OF SUBSTITUTION LINES

Substitution lines and varieties	Thatcher set of substitution lines			Hope set of substitution lines		Timstein set of substitution lines	
	Significantly earlier than Chinese	Same as or similar to Chinese	Significantly later than Chinese	Significantly earlier than Chinese	Same as or similar to Chinese	Significantly earlier than Chinese	Same as or similar to Chinese
I	61.6**				65.5		65.9
II	62.8**			60.4**		63.7**	
III	61.5**			59.3**		64.4**	
IV		66.5		62.1**		65.2**	
V	62.9**			61.7**		62.8**	
VI	61.8**				63.5	62.5**	
VII	62.9**			56.6**		64.7*	
VIII	62.2**				65.0	62.1**	
IX	63.7**			59.1**		65.1*	
X		65.5		59.2**			66.1
XI		67.1			65.6		65.4
XII	61.5**			60.5*		61.4**	
XIII			85.3**	—	—	—	—
XV	65.3*				64.7		66.4
XVI		67.2			65.5		66.5
XVII					64.7	64.5*	
XVIII			87.0**	60.1**		63.0**	
XIX		65.9			68.3	64.9*	
XX		65.9			65.6	63.4**	
XXI		65.6		60.2**			66.6
Chinese		66.9			66.3		66.3
Thatcher		59.2			—		—
Hope		—			61.3		—
Timstein		—			—		56.0
L.S.D. 5% level		1.6			4.1		1.1
S.D. 1% level		2.5			5.4		2.9

* Significant at the 5% level.
** Significant at the 1% level.

values are 2-year (1953–54) averages. The Thatcher averages will not necessarily correspond to the Thatcher values in Tables 1 to 8, which are 3-year (1952–54) averages. The 1952 averages for Thatcher were excluded from this description in order that all comparisons might be on the basis of similar tests.

Experimental Methods

Production of Substitution Lines

The procedure of chromosome substitution has been described previously by Sears (44). The substitution lines used for the genetic investigations reported in this paper were developed by backcrossing to Chinese five or six times (depending on the substitution line), followed by selfing, thus reconstituting the genotype of Chinese approximately 97 and 98 per cent respectively with respect to the 20 Chinese chromosomes not involved in the transfer.

Statistical Design and Analysis of Experiments

A randomized block design with four replicates for the Thatcher substitution lines and the donor and recipient varieties as checks, was used at Edmonton in 1952. In 1953 and 1954, at Edmonton, all three sets of substitution lines were tested in contiguous randomized blocks. The data for each of the characters studied, except awning, were analysed

TABLE 3.—LODGING SCORES OF CHINESE, THATCHER, HOPE, TIMSTEIN, AND OF THATCHER, HOPE, AND TIMSTEIN SETS OF SUBSTITUTION LINES

Substitution lines and varieties	Thatcher set of substitution lines		Hope set of substitution lines		Timstein set of substitution lines	
	Significantly greater lodging resistance than Chinese	Same as or similar to Chinese	Significantly greater lodging resistance than Chinese	Same as or similar to Chinese	Significantly greater lodging resistance than Chinese	Same as or similar to Chinese
I	8.6**		6.4*		7.0**	
II	7.5**		7.7**			6.2
III	6.4**		7.6**			5.4
IV	5.8**		6.0*		6.5*	
V	7.7**		7.1**		7.9**	
VI	6.5**		6.5*			6.0
VII	6.7**		7.7**			5.8
VIII	8.1**		6.9**		8.1**	
IX	7.4**		7.9**		8.0**	
X		4.1		5.4		
XI		4.2		3.0		5.5
XII	5.9**		7.3**		6.3*	
XIII	6.6**		—	—	—	—
XV		4.5		4.6	6.4*	
XVI	5.5**			5.0		5.4
XVII	—	—	6.2*			6.2
XVIII		4.6		5.0	6.4*	
XIX	5.7**		6.3*		7.9**	
XX	6.2**			3.7		4.1
XXI	6.7**		7.5**			4.6
Chinese	4.0		4.0		4.4	
Thatcher	9.8		—		—	
Hope	—		9.4		—	
Timstein	—		—		9.7	
L.S.D. 5% level	1.1		1.9		1.9	
S.D. level 1%	1.4		2.6		2.6	

* Significant at the 5% level.
** Significant at the 1% level.

TABLE 4.—AVERAGE PLANT HEIGHT IN INCHES OF CHINESE, THATCHER, HOPE, TIMSTEIN, AND OF THATCHER, HOPE, AND TIMSTEIN SETS OF SUBSTITUTION LINES

Substitution lines and varieties	Thatcher set of substitution lines			Hope set of substitution lines		Timstein set of substitution lines	
	Significantly taller than Chinese	Same as or similar to Chinese	Significantly shorter than Chinese	Same as or similar to Chinese	Significantly shorter than Chinese	Same as or similar to Chinese	Significantly shorter than Chinese
I		44.8			41.2**	45.9	
II		44.0		43.9		45.4	
III		45.6			42.3*	44.2	
IV		44.4		44.9		45.1	
V		43.9		43.9		46.8	
VI		46.6		44.7		44.6	
VII		43.4			41.5*	44.9	
VIII			41.3**		41.5*		41.7*
IX		44.3			41.0**	44.7	
X		44.7		43.6		44.8	
XI	46.8*			44.9		46.5	
XII		45.6			42.3*	44.0	
XIII		45.6		—	—	—	—
XV		44.9		43.8		44.1	
XVI			42.6*			44.9	
XVII		43.4		45.1		45.7	
XVIII		45.6		46.3		44.3	
XIX		45.5		46.3		47.0	
XX		44.5		45.8		43.2	
XXI		44.5		46.0		46.9	
Chinese		44.6		45.2		45.0	
Thatcher		42.1		—		—	
Hope		—		44.9		—	
Timstein		—		—		35.8	
L.S.D. 5% level		2.1		2.9		3.1	
S.D. 1% level		2.8		3.9		4.2	

* Significant at the 5% level.
** Significant at the 1% level.

separately for the three tests as randomized block designs. Also analysis, as for a split-plot design, was conducted for each of the characters earliness, height, lodging, spike density, and yield. In the split-plot analysis varieties were treated as main plots and lines and the interaction, lines × varieties as sub-plots. Because of unusually severe lodging of the 1954 tests at Edmonton, data from this year on plant height, yield, 1000-kernel weight, protein and spike density were not included in the data. In 1954 at Brooks, each of the three sets of substitution lines was tested using a 6-replicate balanced lattice design. To meet the requirements of this design the varieties Chinese, Thatcher, Hope, Timstein, Regent and Red Bobs were added to each of the respective sets of 19 substitution lines. The data for each of the sets were analysed as individual balanced lattice designs, and, as for Edmonton, were also combined in one analysis as a split-plot design. It was not possible to obtain data on earliness and lodging from this test.

The data in Tables 1 to 8 inclusive are the average of three tests (1952–54) for Thatcher substitution lines, and two tests (1953–54) for Hope and Timstein substitution lines.

Methods of Collecting Data

Awning was studied in all three sets of substitution lines. Four classes, depending on the extent of awn development, were employed: (1) awnless; (2) awnletted, if short awnlets were present; (3) apically awned, if short awnlets were present near the base of the spike and the length of awns increased towards the apex, usually the upper half being almost fully awned; (4) awned, when the spike was fully awned.

Date of heading, used as an indication of earliness, was recorded separately for each plot. The material in a plot was considered headed when approximately 75–80 per cent of the leading spikes had just emerged from the boot. Heading of plants in individual plots was extremely uniform, which greatly facilitated recording these data.

Plant height, determined shortly before maturity, was recorded as the height of plants in inches from the ground to the top of the spike. The heights of 15 plants selected at random were averaged for each plot.

Spike density was determined for the leading spikes of 15 different plants in each plot. The average spike density was calculated by dividing the number of spikelets per spike by spike length, measured in centimetres, from the base of the rachis to the tip of the uppermost spikelet, not including the awns. All nodes were included in the count to give the true number of spikelets.

The average 1000-kernel weight, in grams, of each line was obtained by averaging the weights of three random 200-kernel samples from the seed of each line.

Lodging resistance was recorded at intervals during a period from approximately four weeks after heading to maturity. An average value for each plot was obtained from six observations. A scoring range of 1 to 10

was used. Plots completely lodged were scored "1", those showing lodging of approximately 20 degrees were scored "7–8", and plots standing perfectly erect were given a score of "10".

Yield in grams per plot was obtained on the two centre rod long (16.5') rows of each plot.

Protein content was determined on random samples from each substitution line. The nitrogen content was determined using the Kjeldahl method, on two 1- to 1½-gram samples from each random sample. The values of the two determinations were averaged and multiplied by 4.93 to give the per cent protein content.

EXPERIMENTAL RESULTS

Awning

Data on the effects of whole chromosome substitutions on awning in each of the three sets of substitution lines are summarized in Table 1.

Three types of awn expression were found in the three sets of substitution lines. Illustrations of these awn types along with those of the recipient and donor varieties for each set are shown in Figure 1.

TABLE 5.—PROTEIN CONTENT OF CHINESE, THATCHER AND OF THATCHER SET OF SUBSTITUTION LINES

Substitution lines and varieties	Thatcher set of substitution lines	
	Same as or similar to Chinese	Significantly higher protein content than Chinese
I	14.1	
II	14.7	
III	14.4	
IV	14.6	
V		15.3**
VI	14.4	
VII		15.2**
VIII	14.3	
IX		15.1**
X	14.5	
XI	14.7	
XII	14.1	
XIII	14.1	
XV		15.0**
XVI		15.3**
XVIII	14.5	
XIX	14.1	
XX	14.7	
XXI	14.8	
Chinese	14.2	
Thatcher	14.9	
L.S.D. 5% level		0.60
S.D. 1% level		0.80

** Significant at the 1% level.

The awning data obtained in the Hope set of substitution lines are relatively simple to interpret. The two varieties Chinese and Hope obviously differ only by the genes on chromosomes VIII and X. Since it is known that awn development is largely inhibited in Chinese by the dominant genes Hd and B_2 on chromosomes VIII and X respectively (39, 56), the results clearly indicate that these chromosomes of Hope must carry the recessive alleles permitting or promoting awn development. The genotypes and phenotypes of this cross can then be tentatively indicated as follows:

Chinese: Hd Hd (VIII), b_1 b_1 (IX), B_2 B_2 (X), awnless;
Chinese (*2 VIII Hope*): hd hd (VIII), b_1 b_1 (IX), B_2 B_2 (X), apically awned because only one dominant pair for awn suppression is present;
Chinese (*2 X Hope*): Hd Hd (VIII), b_1 b_1 (IX), b_2 b_2 (X), apically awned because only one dominant pair for awn suppression is present;
Hope: hd hd (VIII), b_1 b_1 (IX), b_2 b_2 (X), awned because no dominant awn suppressor is present.

When chromosome III, VIII, and X of the awnletted variety Timstein are substituted for their homologues in Chinese the substitution lines carrying these chromosomes exhibit apical awning. The remaining 16 substitution lines tested are as awnless as the recipient variety. Since Chinese (2 VIII Timstein) and Chinese (2 X Timstein) show apical awning it seems that chromosomes VIII and X of Timstein carry the recessive alleles hd and b_2 respectively. Chinese (2 IX Timstein) is, like the recipient variety, awnless and on the basis of this and the fact that Timstein is awnletted and carries the alleles hd and b_2, it is assumed that chromosome IX of Timstein carries the allele B_1. However, it could carry another allele slightly less effective, B_1^a. On the basis of these assumptions the genotypes of Timstein and Chinese substitution lines with Timstein chromosomes VIII, IX and X would be as follows—*Timstein:* hdhd$B_1B_1b_2b_2$ or hdhd$B_1^aB_1^ab_2b_2$; *Chinese* (*2 VIII Timstein*): hdhdb_1 b_1 B_2B_2; *Chinese* (*2 IX Timstein*): HdHd$B_1B_1B_2B_2$ or HdHd$B_1^aB_1^aB_2B_2$; *Chinese* (*2 X Timstein*): HdHd$b_1b_1b_2b_2$.

Seven of the 19 Thatcher substitution lines tested expressed awning. Chinese (2 III Thatcher), Chinese (2 IV Thatcher), Chinese (2 XII Thatcher) and Chinese (2 XXI Thatcher) lines were apically awned and

Figure 1—Awn types of the recipient and donor varieties and awned substitution lines in each of the the three sets of substitution lines.

1. Spikes from awnless recipient variety, Chinese
2. Spikes from awnletted donor variety, Thatcher
3. Spikes from awned donor variety, Hope
4. Spikes from awnletted donor variety, Timstein
5. Spikes from apically awned Chinese (2 III Thatcher)
6. Spikes from apically awned Chinese (2 IV Thatcher)
7. Spikes from apically awned Chinese (2 VIII Thatcher)
8. Spikes from awnletted Chinese (2 IX Thatcher)
9. Spikes from apically awned Chinese (2 X Thatcher)
10. Spikes from apically awned Chinese (2 XII Thatcher)
11. Spikes from apically awned Chinese (2 XXI Thatcher)
12. Spikes from apically awned Chinese (2 VIII Hope)
13. Spikes from apically awned Chinese (2 X Hope)
14. Spikes from apically awned Chinese (2 III Timstein)
15. Spikes from apically awned Chinese (2 VIII Thatcher)
16. Spikes from apically awned Chinese (2 X Thatcher)

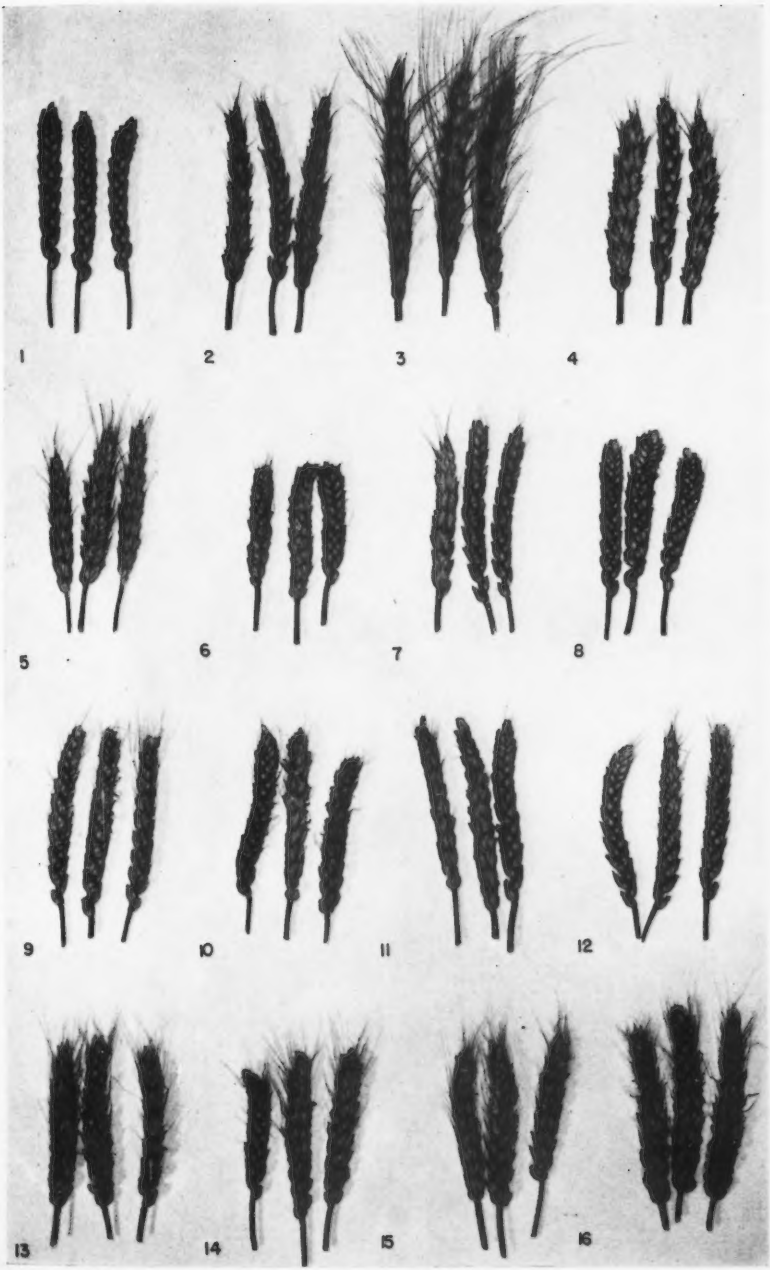

FIGURE 1.

TABLE 6.—SPIKE DENSITIES EXPRESSED AS NUMBER OF SPIKELETS PER CENTIMETRE LENGTH OF SPIKE OF CHINESE, THATCHER, HOPE, TIMSTEIN, AND OF THATCHER, HOPE, AND TIMSTEIN SETS OF SUBSTITUION LINES

Substitution lines and varieties	Thatcher set of substitution lines			Hope set of substitution lines			Timstein set of substitution lines		
	Significantly denser than Chinese	Same as or similar to Chinese	Significantly less dense than Chinese	Significantly more dense than Chinese	Same as or similar to Chinese	Significantly less dense than Chinese	Significantly more dense than Chinese	Same as or similar to Chinese	Significantly less dense than Chinese
I			2.91*		3.12			3.06	
II		3.05		3.52*				3.30	
III			2.77**		3.04				2.79**
IV	3.47*				3.10			3.30	
V		2.99			2.98				2.92**
VI			2.80**		2.88				2.93**
VII		3.04			2.99				2.99*
VIII			2.83**			2.65*			2.93*
IX			2.79**		3.36			3.25	
X			2.69**			2.48*			2.92**
XI		3.08			3.03				2.86**
XII		2.94			3.39		3.43**		
XIII		3.11		—	—	—	—	—	—
XV		3.18			3.04			3.22	
XVI		3.30			3.24				3.00*
XVII		—			2.92			3.07	
XVIII		3.25			3.40			3.22	
XIX			2.91*		3.03				2.93**
XX		3.05				2.67*			2.48**
XXI			2.78**		2.98				2.98*
Chinese		3.20			3.13			3.18	
Thatcher		2.21			—			—	
Hope		—			2.15			—	
Timstein		—			—			1.91	
L.S.D. 5% level		0.27			0.33			0.18	
S.D. 1% level		0.37			0.46			0.25	

* Significant at the 5% level.
** Significant at the 1% level.

Chinese (2 VIII Thatcher) and Chinese (2 IX Thatcher) lines were awn-letted; the remaining 12 lines were awnless. On the basis of awn type it is assumed that Thatcher chromosome VIII carries the recessive allele hd or the allele Hd^a and chromosome IX carries the allele $b_1{}^a$. Chinese (2 X Thatcher) was apically awned as in the previous two sets and most likely Thatcher chromosome X carries the recessive allele b_2. The genotypes with respect to chromosomes VIII, IX and X of Thatcher, Chinese (2 VIII Thatcher), Chinese (2 IX Thatcher) and Chinese (2 X Thatcher) would be as follows—*Thatcher:* $hdhdb_1{}^ab_1{}^ab_2b_2$ or $Hd^aHd^ab_1{}^ab_1{}^ab_2b_2$; *Chinese (2 VIII Thatcher)*: $hdhdb_1b_1B_2B_2$ for $HdHdb_1{}^ab_1{}^aB_2B_2$; *Chinese (2 IX Thatcher)*: $HdHdb_1{}^ab_1{}^aB_2B_2$; *Chinese (2 X Thatcher)*: $HdHdb_1b_1b_2b_2$.

The results from the three sets of substitution lines for chromosomes VIII, IX, and X substantiate previous findings. The appearance of awn types in lines carrying chromosomes III, IV, XII, and XXI of Thatcher and III of Timstein were not expected on the basis of published information. Because genes on the above four chromosomes affect awning, a new hypothesis or an extension of the old one is necessary to explain the results obtained.

It is assumed that either hd or b_2 or both together are epistatic to genes on chromosomes III, IV, XII, and XXI and that Hd or B_2 or both together are non-epistatic or only partially epistatic to genes on chromosomes III, IV, XII, and XXI which may be designated $A_1A_2A_3$ and A_4 respectively. The hypothesis holds whether the genes on III, IV, XII and XXI are dominant or recessive. There may be more than one gene per chromosome, the assumption is made that only one gene affecting awning is present on each of the above chromosomes. We may take chromosome III of Timstein to demonstrate the hypothesis. In the donor parent genes on chromosome III are inhibited by hd and b_2. When chromosome III is substituted into Chinese the action of genes on the transferred chromosome is not inhibited because Chinese possesses Hd and B_2 and the substitution line is apically awned. The same explanation would hold for genes on chromosomes III, IV, XII, and XXI of Thatcher.

On the basis of this hypothesis the genotypes for Chinese, Thatcher, Timstein, and Chinese substitution lines III, IV, XII, and XXI involving Thatcher and Timstein chromosomes would be as follows:

(1) *If awning genes on chromosomes III, IV, XII, and XXI are recessive:*

	III	IV	VIII	IX	X	XII	XXI
Chinese	A_1A_1	A_2A_2	HdHd	b_1b_1	B_2B_2	A_3A_3	A_4A_4
Thatcher	a_1a_1	a_2a_2	Hd^aHd^a or hdhd	$b_1{}^ab_1{}^a$	b_2b_2	a_3a_3	a_4a_4
Timstein	a_1a_1	A_2A_2	hdhd	B_1B_1 or $B_1{}^aB_1{}^a$	b_2b_2	A_3A_3	A_4A_4
Chinese (2 III Thatcher)	a_1a_1	A_2A_2	HdHd	b_1b_1	B_2B_2	A_3A_3	A_4A_4
Chinese (2 III Timstein)							
Chinese (2 IV Thatcher)	A_1A_1	a_2a_2	HdHd	b_1b_1	B_2B_2	A_3A_3	A_4A_4
Chinese (2 XII Thatcher)	A_1A_1	A_2A_2	HdHd	b_1b_1	B_2B_2	a_3a_3	A_4A_4
Chinese (2 XXI Thatcher)	A_1A_1	A_2A_2	HdHd	b_1b_1	B_2B_2	A_3A_3	a_4a_4

(11) *If awning genes on chromosomes III, IV, XII, and XXI are dominant:*

	III	IV	VIII	IX	X	XII	XXI
Chinese	a_1a_1	a_2a_2	HdHd	b_1b_1	B_2B_2	a_3a_3	a_4a_4
Thatcher	A_1A_1	A_2A_2	Hd^aHd^a or hdhd	$b_1^ab_1^a$	b_2b_2	A_3A_3	A_4A_4
Timstein	A_1A_1	a_2a_2	hdhd	B_1B_1 or $B_1^aB_1^a$	b_2b_2	a_3a_3	a_4a_4
Chinese (2 III Thatcher) Chinese (2 III Timstein)	A_1A_1	a_2a_2	HdHd	b_1b_1	B_2B_2	a_3a_3	a_4a_4

	III	IV	VIII	IX	X	XIII	XXI
Chinese (2 IV Thatcher)	a_1a_1	A_2A_2	HdHd	b_1b_1	B_2B_2	a_3a_3	a_4a_4
Chinese (2 XII Thatcher)	a_1a_1	a_2a_2	HdHd	b_1b_1	B_2B_2	A_3A_3	a_4a_4
Chinese (2 XXI Thatcher)	a_1a_1	a_2a_2	HdHd	b_1b_1	B_2B_2	a_3a_3	A_4A_4

It is believed that this or some other multiple gene hypothesis is necessary to explain the occurrence of awn types in so many different substitution lines.

Earliness

Data on earliness in each of the three sets of substitution lines are summarized in Table 2.

The effects on earliness of substituted chromosomes may be divided into three classes, if it is assumed that differences in earliness at or exceeding the 5 per cent level of significance are the result of genes introduced by the transferred chromosome. The various substitution lines can then be placed in the following classes: (a) those significantly earlier than Chinese; (b) those the same as or similar to Chinese; and (c) those significantly later than Chinese.

Results for substitution lines which are similar to Chinese in earliness may be interpreted in two different ways: (a) the genes on the chromosomes of the donor varieties are similar to those on the homologous Chinese chromosomes, or (b) there are no genes affecting earliness carried by these chromosomes in Chinese or the donor varieties. The latter interpretation would likely apply to substitution lines for chromosomes XI and XVI in all three sets, since they were not significantly different from Chinese in earliness.

Ten Thatcher, 10 Hope, and 13 Timstein substitution lines were significantly earlier than the recipient variety. The degree of increase in earliness varied with the individual chromosomes.

Chromosomes hastening earliness of Chinese by five or more days (exceeding the 1 per cent level) were I, III, VI, XII of Thatcher, II, III, VII, IX, X, XII, XVIII, XXI of Hope, and VIII and XII of Timstein. The most striking results were obtained with Hope chromosome VII which advanced the heading date of Chinese by 10 days, causing the line to transgress the earliness of the early donor variety Hope. Chromosomes II, V, VII, VIII of Thatcher, IV, V of Hope and V, VI, VIII of Timstein advanced heading of Chinese by $3\frac{1}{2}$ to $4\frac{1}{2}$ days. Chromosomes IX, XV of Thatcher, and II, III, IV, VII, IX, XVII, XIX, XX of Timstein caused

1½ to 3 days' advance in heading date. Apparently chromosomes V and XII and possibly II and VI of the three donor varieties possessed the same allele(s) since heading date in every case was hastened by 5 to 6 days. Results show that different chromosomes within each set have unequal genetic effects on this character.

The behaviour of Chinese lines carrying Thatcher chromosomes XIII and XVIII is most striking. Throughout most of the summer of each year of testing these lines behaved as true or almost true winter wheats heading approximately 20 to 25 days later than Chinese. The genetic explanation for these results is probably as follows: Chinese carries dominant spring-growth-habit genes on chromosomes XIII and XVIII, while Thatcher carries recessive alleles for winter-growth-habit on these same chromosomes. It has been observed that monosomic XVIII of Chinese produces considerably later heading than does disomic Chinese. When chromosome XVIII of Thatcher is substituted for its homologue in Chinese, plants with near winter growth habit result.

The difference in genetic make-up of homologous chromosomes from different varieties is clearly demonstrated by the highly significant 'lines × varieties' interaction (1953: $F = 41.18$, $5\% = 1.51$, $1\% = 1.79$; 1954: $F = 124.82$, $5\% = 1.64$, $1\% = 2.00$). The chromosomes having different effects are I, II, III, IV, VI, VII, VIII, IX, X, XVIII, XIX, XX, and XXI. Taking chromosome VII as an example we see that Chinese (2 VII Hope) heads in 56.6 days, whereas Chinese (2 VII Thatcher) and Chinese (2 VII Timstein) head in 62.9 and 64.7 days respectively. If the chromosomal effect is due to a single gene, then there appears to be a multiple allelic series for each of these genes on the above chromosomes which would account for the highly significant differences among Chinese lines possessing homologous chromosomes from different donor varieties. Therefore, whether a chromosome from a particular variety will increase or decrease earliness will depend on the particular allele it carries in relation to the one present in the recipient variety. However, the effect of a chromosome may be due to two or more genes. For each of these a double or multiple allelic series may exist. This condition cannot at present be distinguished from a multiple allelic series for a single gene.

Earliness of individual lines was consistent from year to year as shown by non-significance of the 'lines × year' interaction ($F = 0.25$, $5\% = 1.77$, $1\% = 2.25$).

On the basis of these data two types of earliness genes are apparently operating: (a) those differentiating summer and winter growth habit, as on chromosomes XIII and XVIII, and (b) those that modify the expression of genes in (a) to a greater or lesser extent. Thatcher apparently carries winter growth habit genes on chromosomes XIII and XVIII, while Hope and Timstein possess summer growth habit genes on these chromosomes.

Lodging

Lodging data from each of the three sets of substitution lines are summarized in Table 3.

The donor varieties have much greater lodging resistance than the recipient variety. If lodging is genetically controlled, a number of the substitution lines possessing chromosomes from the more lodging-resistant donor varieties should show less susceptibility to lodging than Chinese. If differences among lines were largely environmental and not genetical, little or no consistency would be expected in individual substitution lines from year to year. Lodging scores were, however, very consistent as indicated by the non-significant 'lines × years' interaction ($F = 0.87$, 5% level = 1.94, 1% level = 2.55). It can be assumed, therefore, that differences among substitution lines were caused by genetic differences affecting this character.

None of the lines was significantly lower in lodging resistance than Chinese.

From Table 3 it is clear that the number of chromosomes from the donor varieties affecting lodging is quite large and that chromosomes from different donor varieties do not all have equal effects. Thus, within the group of Thatcher chromosome lines that show significantly greater lodging resistance than Chinese, there are wide differences in this character. Lines I and XXI serve to illustrate this situation; line I being highly significantly more resistant to lodging than line XXI, while both are significantly stronger strawed than Chinese.

The 'lines × varieties' interaction was highly significant in all years (1953: $F = 5.11$, 5% = 1.51, 1% = 1.79; 1954: $F = 11.25$, 5% = 1.67, 1% = 2.05). The interpretation is similar to that for earliness and plant height; that is to say, homologous chromosomes (I, IV, VII, X, XIX, XX and XXI) from different varieties affect this character significantly differently and indicate the presence of multiple series of major and minor genes. The presence of major genes is indicated by the fact that some chromosomes affect this character much more strikingly than others (i.e., compare I and XXI in the Thatcher set).

Since none of the lines was significantly lower in lodging resistance than Chinese, which is very susceptible to lodging (4.1), it is probable that the recipient variety possesses most of the genes for susceptibility to lodging. Also, the donor parents appear to possess a maximum number of resistance genes (average lodging scores of Thatcher, Hope and Timstein are 9.8, 9.4 and 9.7 respectively). Since quite a large number of chromosome lines are significantly more resistant to lodging than Chinese, apparently the effects of most individual genes are small, although not equal. From these studies, it is apparent that lodging is a genetically complex character affected by at least 15 genes or groups of genes.

Plant Height

Data on plant height for each set of substitution lines are summarized in Table 4.

Plant heights of individual lines were consistent from year to year as indicated by the non-significant 'lines × years' interaction ($F = 0.85$, 5% = 1.94, 1% = 2.55). It may, therefore, be assumed that differences between substitution lines at or exceeding the 5% level of significance are

largely genetical. On this basis three phenotypic classes may be assumed: (a) those significantly taller than Chinese; (b) those approximately equal in height to Chinese, and (c) those significantly shorter than Chinese, (Table 8).

Only line Chinese (2 XI Thatcher) was significantly taller than Chinese. Apparently in Thatcher this chromosome carries the strongest height-increasing genes.

Since the donor varieties Timstein, Thatcher, and Hope are shorter than Chinese by 9.20, 2.50, and 0.30 inches respectively, most of the lines deviating significantly from Chinese should be shorter. Results conform to expectation. Chinese lines possessing chromosome VIII from all three donor varieties were significantly shorter than Chinese. Other lines with heights similar to chromosome VIII lines were: Chinese (2 XVI Thatcher), Chinese (2 I Hope), Chinese (2 III Hope), Chinese (2 VII Hope), Chinese (2 IX Hope), and Chinese (2 XII Hope).

Significant height transgression beyond the upper limits of both parents was observed in the Thatcher set and beyond the lower limit of Hope, the shorter parent, in the Hope set of substitution lines.

Certain homologous chromosomes of the donor varieties have different genetic effects from each other. This is clearly shown by the significant 'lines × varieties' interaction (1953: F = 3.63, 5% level = 1.51, 1% level = 1.79; 1954: F = 3.69, 5% level = 1.64, 1% level = 2.01). Chromosome having different effects are III, V, VI, VII, IX, X, XII, and XVIII. Taking chromosomes XII as an example, in 1954 Chinese (2 XII Hope) was 42.0 inches tall, Chinese (2 XII Timstein) and Chinese (2 XII Thatcher) were 42.3 and 50.0 inches tall respectively. Control of plant height appears to be similar to that of earliness in which allelic series or multiple loci or both are operating. Since lines involving eight different chromosomes gave significant height responses, at least eight genes or groups of genes affect this quantitative character in these substitution series.

Protein Content

Data on protein content of Thatcher, Chinese, and Chinese lines with substituted Thatcher chromosomes are summarized in Table 5.

Although protein content is known to be greatly influenced by environmental conditions the results for individual lines were consistent from year to year.

Lines Chinese (2 V Thatcher), Chinese (2 VII Thatcher), Chinese (2 IX Thatcher), Chinese (2 XV Thatcher) and Chinese (2 XVI Thatcher) were significantly higher in protein content than Chinese. They were also higher in protein content than Thatcher though not significantly so. None of the nineteen lines tested was significantly lower in protein content than the recipient variety.

Since five different Thatcher chromosomes were responsible for significantly increasing the protein content of Chinese, at least five genes or groups of genes affect this character in this set of substitution lines.

TABLE 7.—1000-KERNEL WEIGHTS IN GRAMS OF CHINESE, THATCHER, HOPE, TIMSTEIN, AND OF THATCHER, HOPE, AND TIMSTEIN SETS OF SUBSTITUTION LINES

Substitution lines and varieties	Thatcher set of substitution lines			Hope set of substitution lines		Timstein set of substitution lines	
	Significantly heavier than Chinese	Same as or similar to Chinese	Significantly lighter than Chinese	Significantly heavier than Chinese	Same as or similar to Chinese	Significantly heavier than Chinese	Same as or similar to Chinese
I	29.6**			27.0**		26.4**	
II		24.3			24.8		24.3
III		24.4			25.8		23.8
IV		22.7		26.1*			24.4
V	25.7*				24.9	26.5**	
VI		24.4		26.8*		25.8*	
VII		23.4			24.2		22.3
VIII		24.1			22.0		24.2
IX		23.1			24.0		21.6
X		21.1			23.1	25.2*	
XI		23.0			22.6		23.9
XII		23.1			25.0		23.1
XIII		22.7		—	—	—	—
XV		22.0			23.0		21.5
XVI			19.3*		22.7		23.3
XVII	—	—	—		24.0		22.9
XVIII		20.3			20.5		22.8
XIX		23.3			23.6	25.6*	
XX		22.3			21.4		22.1
XXI		23.8			24.1		24.3
Chinese		22.7		22.6		22.8	
Thatcher		31.3		—		—	
Hope		—		36.5		—	
Timstein		—		—		35.6	
L.S.D. 5% level		3.00		3.3		2.4	
S.D. 1% level		4.00		4.4		3.2	

* Significant at 5% level.
** Significant at 1% level.

Spike Density

Data on spike density for each of the three sets of substitution lines are summarized in Table 6.

Donor varieties in all cases had less dense spikes than the recipient variety. None of the lines was as lax as the donor parents; most lines were less dense or as dense as Chinese. Spike densities of individual lines were consistent from year to year as shown by the non-significance of 'lines × years' interaction (F = 0.15, 5% level = 1.94, 1% level = 2.55).

Three lines, Chinese (2 IV Thatcher), Chinese (2 II Hope), and Chinese (2 XII Timstein) transgressed the spike density of Chinese by being significantly more dense. Thatcher chromosome IV apparently carries genes decreasing spike length with number of spikelets remaining the same as in Chinese. Hope chromosome II and Timstein chromosome XII caused a decrease in spikelet number and spike length.

Thatcher chromosomes I, III, VI, VIII, IX, X, XIX, XXI; Hope chromosomes VIII, X, XX, and Timstein chromosomes III, V, VI, VII, VIII, X, XI, XVI, XIX, XX, XXI produce lines with significantly less dense spikes than Chinese. Lines Chinese (2 x Thatcher), Chinese (2 VIII Hope), Chinese (2 XX Hope) and Chinese (2 XX Timstein) had spike density values 0.5 to 0.7 (15 to 22 per cent) lower than Chinese.

Effects of chromosomes within sets of substitution lines were not equal. This indicates that each of a number of chromosomes within any variety may or may not possess modifiers having major and minor effects. The degree to which any variety will be more or less dense than any other will depend on the number of accumulated modifying genes having major and minor effects.

That homologous chromosomes from different varieties are, in some cases, significantly different in genetic effects from each other is substantiated by a highly significant 'lines x varieties' interaction (1953: F = 23.18, 5% level = 1.48, 1% level = 1.75; 1954: F = 3.49, 5% level = 1.69, 1% level = 2.10). This significant interaction may support either of two alternatives: (a) individual chromosomes affect spike density due to one gene per chromosome with a series of two or more alleles; (b) each chromosome may possess two or more genes and each of these may possess a series of two or more alleles.

Spike density among *vulgare* varieties is affected by chromosomes possessing minor genes which influence spike denseness to a variable degree.

Thousand-Kernel Weight

Data on 1000-kernel weight in each of the three sets of Chinese substitution lines are summarized in Table 7.

The donor parents, Thatcher, Hope, and Timstein, were each significantly heavier (5 per cent level) in thousand-kernel weight than Chinese. Chinese (2 XVI Thatcher) was the only line that was significantly lower than the recipient variety. The following lines were significantly heavier (5 per cent level) than Chinese: Chinese (2 I Thatcher), Chinese (2 V

TABLE 8.—YIELDS IN GRAMS OF CHINESE, THATCHER, HOPE, TIMSTEIN, AND OF THATCHER, HOPE, AND TIMSTEIN SETS OF SUBSTITUTION LINES

Substitution lines and varieties	Thatcher set of substitution lines		Hope set of substitution lines		Timstein set of substitution lines		
	Significantly higher than Chinese	Same as or similar to Chinese	Significantly higher than Chinese	Same as or similar to Chinese	Significantly higher than Chinese	Same as or similar to Chinese	Significantly lower than Chinese
I	830.7**		707.1**		737.5**		
II		682.0		552.1	543.3*		
III	704.9*			565.9	555.0*		
IV		502.2	580.0*		633.3**		
V		678.3	617.1**		551.7*		
VI		631.4	629.2**		563.9**		
VII		630.9	664.6**		549.6*		
VIII	763.5*		637.9**		703.0**		
IX		637.8	625.9**			483.5	
X		625.7	622.5**				425.2
XI		492.9		462.1		505.6	
XII	721.3*		711.3**		559.8*		
XIII		426.3	—	—			
XV		580.8		545.9		487.1	
XVI		473.1		473.4	582.1**		
XVII	—	—		547.5	545.4*		
XVIII		445.0	—		551.7*		
XIX		647.5		527.1	668.4**		
XX		590.3		503.8		530.6	
XXI		688.7	655.9**		575.7**		
Chinese	523.7		484.6		483.5		
Thatcher	1013.8		—		—		
Hope	—		675.8†		—		
Timstein	—		—		957.9		
L.S.D. 5% level	183.9		83.8		56.4		
S.D. 1% level	246.9		113.4		76.6		

* Significant at 5% level.
** Significant at 1% level.
†Yield of Hope for 1954 only.

Thatcher), Chinese (2 I Hope), Chinese (2 IV Hope), Chinese (2 VI Hope), Chinese (2 I Timstein), Chinese (2 V Timstein), Chinese (2 VI Timstein), Chinese (2 X Timstein), and Chinese (2 XIX Timstein).

It may be assumed, therefore, that at least seven chromosomes, I, IV, V, VI, X, XVI, and XIX, carry genes affecting kernel weight. Chromosome I from all three donor varieties had the greatest effect. In every case the size of kernel was significantly increased by the substitution of this chromosome.

Yield

Data on yield of Thatcher, Hope and Timstein sets of substitution lines are summarized in Table 8.

Certain accessory factors affecting yield such as drought, various diseases and insects, were either not present or reduced to a minimum. However, lodging and other characters such as kernel size varied from line to line and probably affected yield. Despite the presence of some of these factors yields of individual lines were reasonably consistent from year to year ('lines x years' interaction non-significant; $F = 0.07$, $5\% = 1.95$, $1\% = 2.55$).

All three donor varieties outyielded Chinese by 180 to 200 per cent (the Hope yield of 675.8, for 1954 only, was compared with the Chinese yield of 366.7 for that year only and not with the Chinese average through the years 1952 to 1954). None of the lines was higher yielding than the critical donor variety and only one was significantly lower yielding than Chinese.

It is assumed that increase in yield over Chinese at or exceeding the 5 per cent level of significance is the result of genes for yield introduced by the transferred chromosome. According to this assumption, substitution lines may be grouped into two classes, in each set of substitution lines, as shown in Table 8.

(Chinese) 2 X Timstein was the only line significantly lower yielding than Chinese.

The class of chromosome lines that are not significantly different from Chinese includes chromosomes XI, XV, and XX of all three donor varieties plus a number of other chromosomes from each of the donor varieties, (Table 8). It is considered, therefore, that lines involving chromosomes XI, XV, and XX probably carry no differential genes affecting this character.

The number of lines that are significantly different from Chinese varies with the donor varieties. Four Thatcher, 10 Hope and 14 Timstein chromosome lines yielded significantly higher than Chinese. Chromosome lines I, VIII, and XII of all three donor varieties were higher yielding than Chinese. In the set of substitution lines possessing Thatcher chromosomes, line I was the highest yielding (58.6 per cent more than Chinese); however, it was not significantly different from lines III, VIII, and XII. In the Hope set of substitution lines, chromosome I and XII lines were significantly higher yielding than chromosome lines IV, V, VI, VII, VIII, IX, X, and XXI, which were not significantly different from each other.

In the Timstein set results are still more variable. Chromosome I is significantly different from IV and XIX which in turn are significantly different from II, III, V, VI, VII, XII, XVI, XVII, XVIII, and XXI. Chromosome lines of the latter group are not significantly different from each other. These results clearly show that different chromosomes of a variety affect this character unequally, at times significantly so. In the Thatcher set the significantly different lines yielded 34.6 to 58.6 per cent more than Chinese. Most of the Hope chromosome lines yielded 19.7 to 37.0 per cent more than Chinese, only I (45.9 per cent) and XII (46.8 per cent) yielded higher. Ten of the 14 Timstein chromosome lines yielded 12 to 20 per cent higher than the recipient variety, lines I, IV, VIII, and XIX yielded 31 to 52 per cent more than Chinese. Thatcher appears to possess a few major genes for yield while Hope and Timstein appear to carry minor genes mainly with only a few major genes. Chinese seems to have an accumulation of a large number of genes that give low yield, presumably recessives of dominant vigour genes.

Homologous chromosomes IV, VII, IX, XI, XII, XVI, and XIX from the donor varieties are significantly different from each other in genetic effects ('lines x varieties' interaction—1953: $F = 9.07$, $5\% = 1.51$, $1\% = 1.78$; 1954: $F = 5.06$, $5\% = 1.43$, $1\% = 1.66$). As an example, Chinese (2 XII Thatcher) yielded 37.7 per cent more than Chinese, while Chinese (2 XII Hope) and Chinese (2 XII Timstein) yielded 46.8 and 11.8 per cent more, respectively—a difference of 31 per cent between the highest and lowest yielding lines.

On the basis of the results obtained yield is apparently controlled by genes located on at least 14 chromosomes.

DISCUSSION

The results of this study clearly indicate that the use of substitution lines will be as valuable in analysing the genetic basis of quantitative characters as they have been in dealing with qualitative characters.

One main probelm normally encountered in genetic analyses of quantitative characters is the determination of the effect of the environment on the individual segregant. This environmental effect varies with the conditions under which the population is grown making it impossible to obtain consistent results especially when parts of a population are grown in different seasons. When whole chromosome substitution lines are used, the effects of the environment on the character in question can be easily removed, since whole populations of each of the genotypes can be treated as varieties in adequately replicated field experiments. Each line represents a genotype that differs from the genotype of the recipient variety only with respect to the genes carried by the substituted chromosome, and the genetic effects of this chromosome can be compared with the standard on a population basis.

While the main emphasis in this study was on quantitative characters, interesting information was obtained on morphological ones. Awning was studied in this substitution material and it was found that seven Thatcher, two Hope and three Timstein chromosomes affected awning.

The association of awning genes VIII, IX, and X substantiates previous findings (33, 39, 56). An extension of the present hypothesis of the genetic basis of awning is, however, necessary to account for awning in substitution lines III Timstein and III, IV, XII and XXI of Thatcher. The basis suggested for the extension of the present hypothesis actually conforms quite closely to that proposed by Heyne and Livers (20). To determine whether the awning effect of a chromosome is due to single dominant or recessive genes necessitates crossing each of the substitution lines, III, IV, XII and XXI and the recipient variety. Only genes on the critical chromosome pair will segregate. If F_1's are awnless Chinese carries the dominant allele(s), if awned, it carries the recessive allele(s) and the awn-promoting gene is dominant. F_2 segregation will show whether one or more genes on the critical chromosome is conditioning awning. The same method may be used to determine whether one or more genes is responsible for the effect of a chromosome on any other character.

Studies of earliness indicate that time of heading is conditioned (a) by genes that differentiate spring and winter growth habits and (b) by genes that modify the expression of growth habit to a greater or lesser extent. A recessive gene for winter growth habit was associated with chromosome IX of the variety Hymar (56). In this study genes for winter growth habit were associated with chromosomes XIII and XVIII of Thatcher. Growth habit is, therefore, governed by at least three loci, each on a different chromosome. Modifying genes were found to be of varying effectiveness. Ten chromosomes each of Thatcher and Hope and 13 of Timstein increased earliness significantly.

Genes on three Thatcher, six Hope and one Timstein chromosome had marked effects on plant height. Increase in plant height was brought about by a gene or genes on chromosome XI of Thatcher. Chromosomes I, III, VII, IX and XII of Hope, VIII of Thatcher, Hope, and Timestin, and XVI of Thatcher apparently possess genes reducing plant height of the recipient variety Chinese. These results substantiate findings of other workers, Thompson (54) and Sears (39).

Results on spike density substantiate those of other studies (5, 49, 50, 51, 52) in 21 chromosome wheats. Major genes apparently differentiate dense from lax spikes in crosses between *compactum* and *vulgare* types, while within types, the degree of spike density depends on minor genes. Since the substitution series of this study involved *vulgare* types, minor gene differences only would be expected. Chromosome IV of Thatcher, II of Hope and XII of Timstein increased significantly spike density of Chinese, while eight chromosomes of Thatcher, three of Hope and eleven of Timstein significantly reduced spike density. The study of this character indicates clearly that substitution lines analyses can be used successfully to analyse minor gene effects.

In contrast to characters such as earliness and spike density where major genes modified by minor genes are acting, lodging, protein content, 1000-kernel weight and yield were found to be affected by genes on many chromosomes, none of which had major effects. Although the effects of the genes were small they were not equal.

Since whole chromosomes are tested, it is impossible, before further work is carried out, to predict whether the chromosome effect on any character is due to one or more genes. Where substitution lines are not significantly different from Chinese this similarity may be due to absence of pertinent genes on chromosomes concerned or similarity of alleles in both the recipient and donor varieties. Where differences are significant this may be due to one or more differential genes per chromosome.

The chromosome 'line x donor' variety interaction calculated to be significant for the characters earliness, height, lodging, spike density and yield is of interest. The significant interactions indicate, of course, that homologous chromosomes from different varieties are significantly different genetically. Two explanations for these differences may be: (a) the action of a chromosome is due to one gene with two or a series of alleles, the alleles being carried by homologous chromosomes of different varieties; or (b) homologous chromosomes carry more than one gene, and when transferred to Chinese different genetic combinations result.

From the standpoint of the plant breeder these results indicate that it might be possible, and in certain cases economically feasible, to improve existing varieties using whole chromosome substitutions with genes for desirable characters from other varieties. The method will probably be most useful for incorporating characters controlled by one or two genes, such as disease- and insect-resistance, into a single line or variety. Since whole chromosomes are being replaced a concomitant of the improvement for these monogenically and digenically controlled characters may occasionally be a loss of desirable genes for other characters carried on the chromosome of the recipient variety. However, the converse may also be true; the genes of the chromosome of the donor variety may augment or improve the existing desirable character. Before making transfers it is desirable that one of the following precautions be taken: (1) the effect of the donor variety chromosome, carrying the gene or genes for the desirable character, must be determined for all other characters, or (2) a variety must be chosen that possesses as many as possible of the desirable characters of the recipient variety in addition to the one or two that it lacks.

The transfer of single genes, or closely linked gene series, where all desirable alleles are to be found in a suitable donor, is most efficiently performed by the backcross method, the simplest of all conventional breeding methods. However, for such transfers the substitution method is even simpler and more efficient since no inter-backcross selfing or progeny testing is required. Thus results would be obtained more quickly and with smaller plant populations. Other situations, such as those involving the transfer of loosely linked genes increase the population required by the backcross method considerably. Yet, there would be no increase in population size required by the substitution method, since it is not affected by linkage intensity due to the fact that the transferred chromosome is never involved in crossing over because its homologue in the female parent is absent. Naturally, if the chromosome from the donor variety carries a desirable gene linked with an undesirable one, the substitution method could not

be used to incorporate both desirable genes. In such situations a donor variety possessing both desirable genes would have to be synthesized before the method could be used.

The substitution method has yet another advantage. If a chromosome is known to carry a gene or genes for resistance to a disease or insect, this chromosome can be incorporated into a line or variety without going through testing procedures every backcross generation; the final line or variety is tested for the resistance to the disease or insect. Each generation, however, may be tested for resistance if desired. In the backcross method testing for resistance to the disease or insect is required every backcross generation to select the desired types.

The backcross method has the following advantages: (1) it may be employed at any institution, whereas the substitution method could be used only where suitable equipment is available, and (2) if no varieties exist which have both desirable genes linked then the backcross method is the only one that will give the desired results.

It is doubtful if the substitution method would be too successful in improving existing varieties if the character is conditioned by a large number of genes with similar minor effects and these carried by numerous chromosomes. For quantitative characters conventional breeding methods are, it seems, to be preferred to the substitution method in that they will produce, in most cases, as great a desirable effect as the substitution of chromosomes in a much shorter time. In the substitution method only one chromosome may be transferred at any one time into a particular line and it would take many years to combine all the desired substitutions to produce a superior line or variety. In the conventional breeding methods (i.e. pedigree) numerous genes from different chromosomes are selected and maintained throughout the segregating generations and the resulting line or composite of lines would probably have a larger number of genes than a combination of two, three or even more chromosome substitutions and in a shorter time.

When more gene-chromosome associations are established and when gene linkages are determined, the success of the method as a breeding procedure will be more accurately evaluated. It must, however, be realized that the chromosome substitution method is (1) an important method of genetic analysis for polyploid organisms and (2) for characters monogenically or digenically controlled, it probably is as effective a breeding procedure as is the backcross method.

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